ANIMAL LIFE IN DESERTS

A STUDY OF THE FAUNA IN RELATION TO THE ENVIRONMENT

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ILLUSTRATED

LONDON
EDWARD ARNOLD & CO.
1923

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Made and Printed in Great Britain by
Butler & Tanner, *Frome and London*

PREFACE

Circumstances over which I had no control induced me to study the conditions of life in Lower Mesopotamia and in North-West Persia for more than two years. I had previously seen desert life in spring-time during a short visit to Algeria, and more recently I have lived in Jerusalem, a city which is not indeed in the desert, but within easy reach of the deserts of Southern Palestine and of the lower end of the Jordan depression. I have endeavoured to summarize my own observations and to elucidate their meaning by comparison with what has been observed in other deserts. The desert is an environment unspoilt by the hand of man, so that one can more clearly observe the interaction of plant and animal upon each other, and the dependence of the living creatures upon climate and other physical conditions.

This "œcological" study will, I hope, prove interesting to many who delight in natural history, but who have never had an opportunity to make themselves acquainted with the more formal aspects of Zoology. As every reader will discover, the study of the animal in relation to its surroundings is beset with difficulties; we are ignorant of certain details

of the climatology of deserts, and of the life-history of the great majority of the smaller animals, and there is at present a complete absence of experimental work upon them. It is partly in order to summarize our present knowledge and to draw attention to the graver deficiencies in it that this book has been written.

The study of the desert creatures and their environment leads one to a very fascinating meeting-place of several sciences. It can only be approached with the help of botanists, meteorologists, physicists, and others. My debt to my fellow-workers is the greater because the book was written in Jerusalem, without access to a good library; I have therefore been forced to rely on the kindness and generosity of correspondents, many of them unknown to me personally. In many cases I have embodied the information which they have given me, and made no acknowledgment of it in the text, because my purpose has been to eliminate foot-notes and bibliography from a book which can make no claim to completeness.

My friends Mr. C. B. Williams and Mr. V. H. W. Dowson have allowed me to draw upon them for several illustrations. Fig. 11 is from a photograph taken by Mr. F. W. Green, and to him and to the Director of the Geological Survey of Egypt I wish to express my gratitude. For Fig. 32 we are indebted to Dr. R. I. Pocock and the Zoological Society of London; for Fig. 34 to Mr. E. C. Stuart Baker and the Bombay Natural History Society; for Figs. 38 and 41 to Dr. J. Grinnell and the Museum of

Vertebrate Zoology, University of California, U.S.A. I am indebted to the Director of Agriculture, Iraq, for the data on which Fig. 8 is based: I am also extremely grateful to Miss A. M. Gayton and Mr. Engel Terzi for the line drawings. My friends Mr. C. B. Williams and Mr. W. E. Evans gave me invaluable assistance in the preparation of Chapter I (" The Desert Climate ") and Chapter III (" The Floral Environment "). To my wife, my sister, and my mother my best thanks are due for help in preparing the book for the press.

P. A. BUXTON.

JERUSALEM.

June, 1923.

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ANIMAL LIFE IN DESERTS

CHAPTER I

THE DESERT CLIMATE

i. General. ii. Water. iii. Heat. iv. Relative Humidity. v. Wind. vi. Evaporation. vii. Light. viii. Summary.

i. General

A prominent authority has stated that the desert occupies one-fifth of the surface of the globe, an area equal to that of Africa. It is probable that the word desert was used in rather a wide sense, and it is certain that no one has yet arrived at a definition of the word which would be acceptable either to the biologists or to the meteorologists. One is accustomed to think of the desert as an area of the earth rendered unfit for normal life by its climate, but, as I hope to show later, there is no climatic factor, or combination of climatic factors, which invariably produces desert; in fact, a few deserts exist by reason of their geological constitution, though their climate is not particularly unfavourable to plant and animal life. As the causes which result in desert are diverse, it follows that the term is not capable of strict definition: the definition which I now put forward is admittedly

unsound, because it looks not to the forces which produce the desert, but to the result of their action; not to the weather and soil, but to the plants and animals which can grow in the desert in spite of its physical conditions. I use the word "desert" to include places in which the climate is hostile to animals and plants, in which normal agriculture is impossible, and in which nearly all the existent forms of animal and plant life are modified to endure life in their peculiar environment. I use the word "semi-desert," without exact definition, to describe country of which the climate is less hostile, and the flora and fauna less specialized, than that of a desert; semi-deserts support cultivation at certain seasons, and provide grazing, though it is often bad grazing, at all seasons. Let us also bear in mind that deserts grade quite imperceptibly into semi-deserts, and these into savannas, steppes, and downs, and that a country may be extreme desert at one season and covered with lush vegetation at another. Furthermore, deserts are not necessarily permanent or very ancient; the buried civilization of Eastern Persia and Turkestan and the petrified forest near Cairo are sufficient evidence of this.

Most of the extensive deserts lie a little to the north of the northern tropic, or a little to the south of the southern tropic; they do not lie close to the Equator. Most of them lie in the northern hemisphere and are bounded northwards by steppe, that is to say, arid country with a covering of grass and other perennials and an abundant flora

after the winter rain, and southwards by savanna, that is to say, arid grass land with a few trees. The largest of all deserts is practically continuous from the Atlantic coast of North Africa to North-west India and the heart of China. It includes the whole of Northern Africa down to about latitude 20° N., but excluding those parts of Morocco, Algeria, and Tunisia which border the Mediterranean: it includes also Egypt and Sinai; Arabia, the Syrian Desert, and Mesopotamia; Persia, Afghanistan, and Baluchistan; Transcaspia, Turkestan, and the Gobi Desert, in Central China; and parts of the Punjab, Sind, and Rajputana. The whole of this vast area is inhabited by the same types of animals and plants, and these for the most part are derived from Europe and Northern Asia, and to a much smaller extent from equatorial Africa or peninsular India. The great desert is, in fact, an integral part of the "Palæarctic Region," which is one of the primary divisions into which zoologists and botanists have divided the globe: this region includes all Europe, and Northern and Western Asia, and Africa as far south as the southern part of the Sahara (about latitude 20° N.). I propose, therefore, to use the term "Great Palæarctic Desert" when referring to this tract.

The great desert of Australia is probably the second in the world in point of size; it includes the heart of the continent and reaches nearly to the west and south-west coasts.

The North American deserts consist of several small areas in the southern and south-western

States of the Union, and in Mexico. The importance of these deserts to the botanist, and in a secondary manner to the zoologist, lies in the fact that they have been more thoroughly studied than any other desert region in the world. The laboratory at Tucson, Arizona, supported by the Carnegie Institution of Washington, and directed by Dr. D. T. Macdougal, has contributed immensely to our knowledge of the climatic and physical features of the surrounding deserts, and of the influence of these features upon the vegetation.

Other desert areas are found in South-West Africa and along the coast of South America, from latitude 5° to 30° S., in Eastern Patagonia and Western Argentina. Quite small areas of desert occur in many parts of the world, and any area of sand dune very closely resembles desert in the scarcity of available moisture, and in the specialization of its flora.

It is not to be understood that any area described above as desert is uniformly so, either in its physical condition or in its flora and fauna. In the belt occupied by the Great Palæarctic Desert there are certain very fertile spots, for example, the delta of the Nile, the highlands of Yemen, and the date groves of Basra, and a similar diversity is found in other desert regions.

We shall now review the climatic influences which contribute largely to make life in a desert impossible to any plant or animal which is not specially adapted to it. In the mind of every one the desert stands first for dryness, secondly for

heat; and though this conception is not strictly accurate, I propose to be guided by it. I shall therefore deal first with the supply of water and second with the heat and cold experienced in deserts. The available moisture and the current temperature together determine the amount of water-vapour present in the air, and I shall deal with this next. This will be followed by some facts relative to winds, because air movement is the result, in part at any rate, of the rapid fluctuations in the temperature to which these bare spaces are subject. The discussion of wind leads us naturally to consider evaporation, which results from the presence of moisture and the combined action of heat and of air movements. The meteorological statistics which are quoted do not give very accurate information of the conditions to which the desert plants and animals are exposed. The instruments with which they are taken are generally exposed in a ventilated white-painted screen: the organisms which we are studying live on the surface of rocks, and in holes, and in a variety of other natural habitations.

ii. Water

It may be admitted at once that relative lack of moisture is a characteristic feature of all deserts, but it is not possible to state dogmatically that if the rainfall be below a certain figure the land will be desert, because the condition of the land depends not only upon rainfall but on many other climatic factors. It is generally accepted that a rainfall

of less than 5 inches (127 mm.) a year always produces desert. On the other hand, there are areas between the Pacific Ocean and the Californian ranges of mountains, and in the Jordan Valley, which are desert though they receive 18 inches (460 mm.) of rain. In the first area the causes are the very high winds to which it is exposed, and the fact that most of the rain falls in winter, when it is of little service to the plants. In the second area, the lower end of the Jordan Valley and the land round the Dead Sea, the cause is the salinity of the soil. One concludes that it is unprofitable to devote much attention to the mean annual rainfall because the number of inches received is of less importance than certain peculiarities in its distribution through the seasons and through successive years, and because such factors as soil and exposure are also of prime importance.

The rainfall in deserts is always very unevenly distributed throughout the months and the seasons, and unless one or more dry seasons of several months' duration occur, the condition of the land is not desert or even semi-desert. The graph (Fig. 1) shows the seasonal distribution of the rainfall which is characteristic of most places in the Great Palæarctic Desert. It will be seen that there is a dry or nearly dry season in summer, averaging six months, and a relatively wet season in winter. In the deserts of South Australia a similar alternation of dry hot weather and wetter cold weather occurs with regularity.

The fact that the rainless period and the hot

period coincide is of great importance to the vegetation, which has to protect itself simultaneously against drought and heat: furthermore, the dry and hot period is very long.

Within the limits of the Great Palæarctic Desert there are a few places which do not have a cold

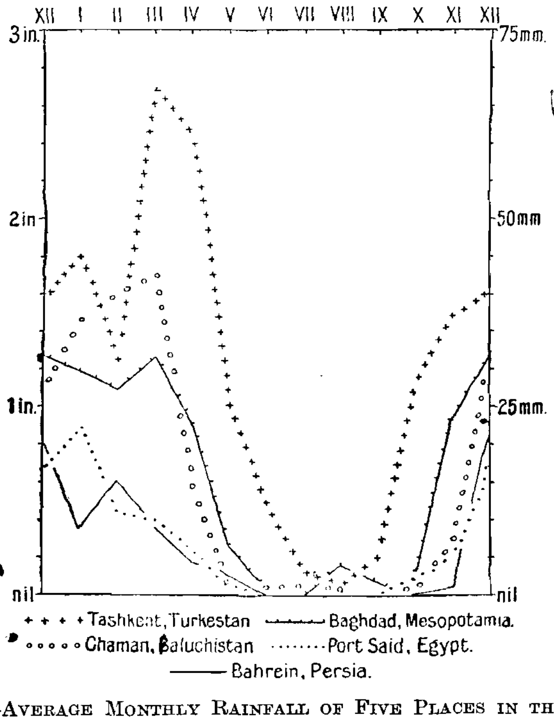


Fig. 1.—Average Monthly Rainfall of Five Places in the Great Palæarctic Desert.

wet season and a hot dry season. The area of the Indian desert (Fig. 2), in Rajputana, Sind, and the Punjab, is an exception, as owing to the monsoon the majority of its rain falls in July or August: in most stations in this area a small fall of rain occurs also in early spring.

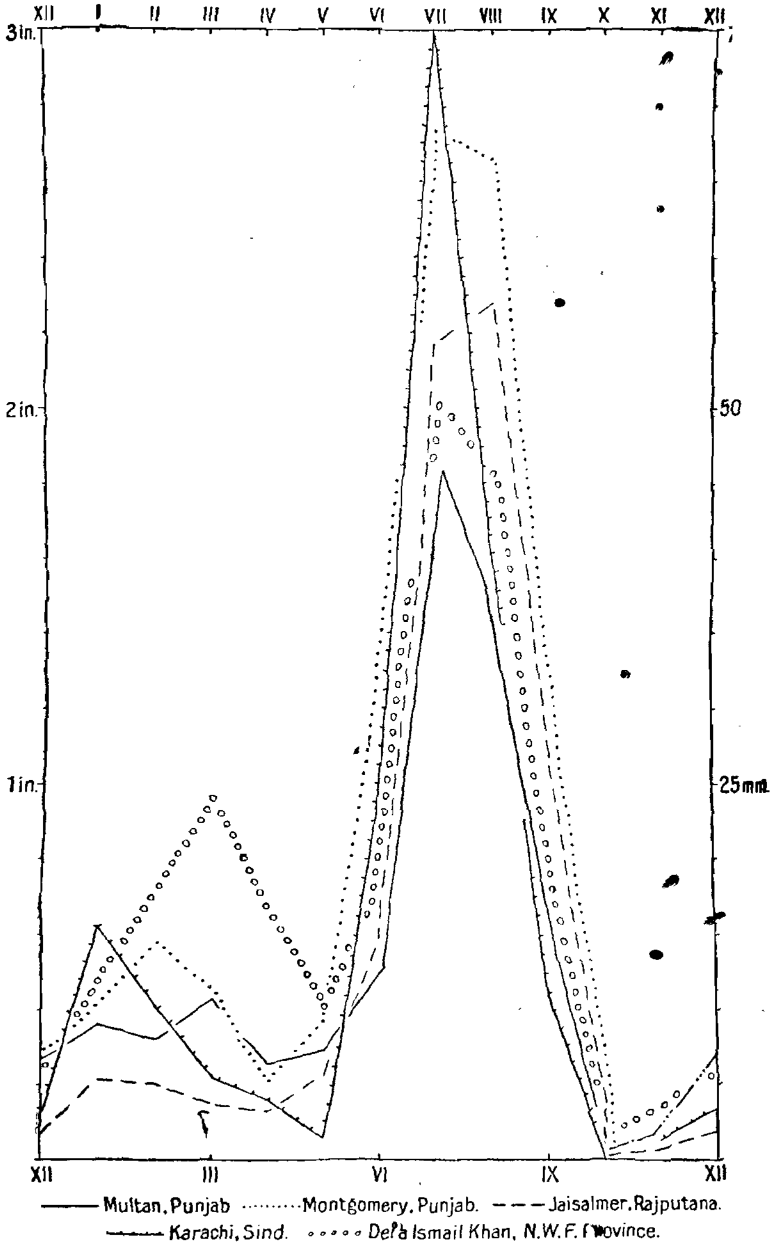


Fig. 2.—AVERAGE MONTHLY RAINFALL OF FIVE PLACES IN THE INDIAN DESERT.

At many stations in the North American deserts the distribution of the rainfall resembles that which has just been described in the Indian desert (Fig. 3). The heaviest fall occurs in the summer, and a definite winter rain occurs in many places, so that

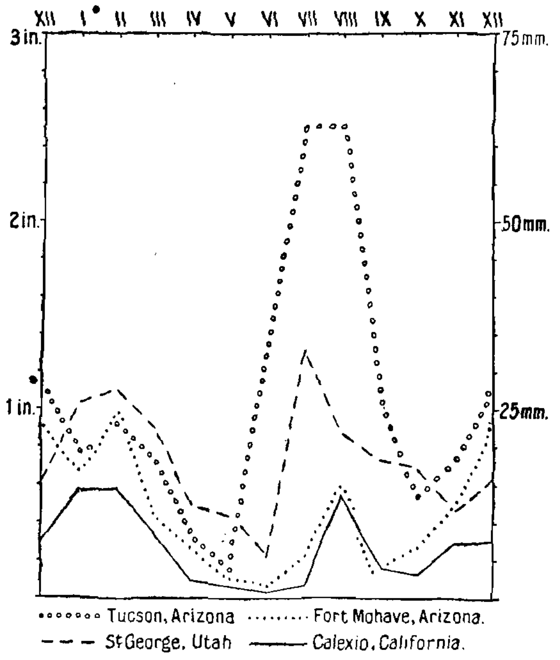


Fig. 3.—Average Monthly Rainfall of Four Places in the Deserts of the Southern States of the U.S.A.

The distribution of rainfall shown in this graph is not characteristic of stations in every part *of these deserts.*

there are two short dry seasons, in early summer and in autumn, in the North American and in the Indian deserts. At a large number of stations in the arid parts of North America only one rainy season is recorded, either in midsummer or in midwinter.

So far, then, as moisture is concerned the conditions

in the deserts of India and in some of those of North America are much less rigorous than they are in most parts of the Great Palæarctic Desert: firstly, because the season of great heat is not also the season of great drought; secondly, because the periods of drought are shorter as there are two dry and two wet seasons in the year; and, thirdly, because in the majority of stations a little rain falls in nearly every month of an average year. If the rainfalls which are shown graphically in Figs. 1–3 are studied it will be seen that either one or two dry periods per year is characteristic of all the places. In certain places these dry periods are much more extended, for the precipitation is quite irregular in its occurrence, and an intense desert results. Hayward found mimosas dead at Kidal in the South Sahara after five years without rain; one must suppose that, as trees had been able to grow, the normal conditions were not utterly unfavourable to plant life, but an unusually long dry spell killed, no doubt, not only the mimosas but other plants as well, and with each plant species a host of insects, spiders, and other animals dependent on it. A year after Hayward made his journey across the Sahara Hartert was in Tidikelt, in the Central Western Sahara (1912). He found that rain had been very deficient for twenty years and as a result the Chenopodiaceous plant *Traganum*, which Rohlfs found growing in thickets in 1864, had died completely, even to the very roots.

Mrs. Forbes has recorded that when she was at Kufara (Libya) in 1921 no rain had fallen for seven

years, and it is probable that throughout a great part of the Libyan Desert and of the Western Sahara the rainfall is so slight and so irregular in its occurrence that it makes little difference to the plant life. Such plants as exist at all, and they are very few, are dependent on subsoil water.

Prolonged droughts have been recorded from many other deserts. As we have seen, the rainfall in the American deserts normally falls twice yearly, and is distributed through nearly every month: in spite of this it is on record that no measureable rain fell at Bagdad, California, from October 3, 1912, to November 8, 1914; a drought of over a year occurred at Indio, California, from November, 1893, to January, 1895.

It may be stated as a general rule that the rainfall in desert places, even in places in which it is relatively regular, is liable to very great variation from the monthly and annual averages. This variation intensifies the struggle between the plants and animals and their environment, and is an important factor in the production of a desert. Angot suggested that the ratio between the maximum and the minimum annual rainfall of a spot could be used as an index of its agricultural possibilities. He believed that conditions were very unfavourable to agriculture in places in which the annual minimum rainfall was less than one-third or one-half of the annual maximum. It is known, however, that an even greater disproportion than this can occur in places which are by no means desert, and we cannot say that a great irregularity in the amount of annual rainfall

is found only in desert areas or that it is an invariable characteristic of the desert climate. It occurs very generally in the more pronounced deserts, and the following are striking examples:

Place.	Annual Rainfall, inches.			Ratio (max. = 100).
	Min.	Av.	Max.	
Salton Sea, California	trace	2·74	7·1	0·1 : 100
El Paso, Texas	2·20	9·23	18·30	12·0 : 100
Yuma, Arizona	0·60	3·26	11·41	5·3 : 100
Mohave, California	2·20	4·97	21·34	10·3 : 100
Tucson, Arizona	5·26	11·58	24·17	21·7 : 100
Wargla, Algerian Sahara	nil	3·55	8·27	0·0 : 100
Beni Ounif, Algerian Sahara	0·50	?	8·50	5·9 : 100
Baghdad, Mesopotamia	2·00	7·29	17·30	11·6 : 100
Basra, Mesopotamia	2·10	6·60	10·70	19·9 : 100
Roeburn, Australia	0·13	?	42	0·32 : 100

It might be supposed that the number of rainy days per month or per year would be closely correlated to the monthly or annual precipitation, but this is not the case, for very great variation occurs in the amount of rain which falls on the average rainy day. In some desert climates it falls in minute amounts, and the number of rainy days may therefore be relatively large. This is characteristic of the South Australian Desert. At Oodnadatta, for instance, one-third or even one-half of the annual precipitation (4·68 inches: 118 mm.) is in amounts of less than 0·15 inch (4 mm.): such minute amounts of water do not moisten the soil to an appreciable depth, and are very quickly evaporated,

unless one minute fall rapidly succeeds another. We need to distinguish between the actual rainfall and that part of it which reaches the roots and so becomes available to plants, and subsequently to animals.

In other desert climates the opposite condition occurs, for the rain falls in large amounts on a very few days in the year. This is characteristic of very many deserts and may be so extreme that a single day's downpour exceeds the total rainfall of an unusually dry year. As examples one may quote the following figures:

Place.	Annual Average		Day's absolute Maximum.		Month.
	in.	mm.	in.	mm.	
Bairam Ali . . .	5·05	128	1·62	44	March
Golodnaia Steppe .	11·05	278	3·97	101	November
Andijan	9·60	242	2·91	61	October
Basra	6·60	167	3·10	78	November
Amara, Mesopotamia	8·0	203	6·75	171	November
Jodhpur, India . .	13·63	347	10·00	253	August

Such excessive rainfall is comparatively unavailable to plants and animals because a great proportion of it runs off the surface of the ground into the river beds, and only a small part soaks into the soil at the place where it fell. The torrent which is produced in the stream bed is extremely destructive to plant and animal life (page 50). I conclude, then, that statistics of the average number of rainy days per month, or year, or of variation

from that average, give little informatior biologist.

It is probable that dew is of extreme importance to the desert flora and fauna, but as practically no reliable statistics relating to actual dew-fall have been published, I am compelled to leave the matter in a very unsatisfactory state. It would be of great interest to biologists if meteorological observatories situated in deserts would accumulate information as to the amount of dew which actually falls under natural conditions, and the seasons and regularity of its fall.

To sum up, the ordinary meteorological statistics are enough to assure us that the aridity of deserts is great; they do not, however, tell us the whole truth, for three reasons. The first is that much of the recorded rainfall is not to be reckoned as "available moisture," because a large proportion falls in heavy downpours which run off the surface of the ground into the water channels, and in some places an equally large proportion falls in such small amounts that it fails to penetrate the soil before it is evaporated. The second reason is that rain which falls in the cold season, when vegetation is inactive, is of little value to the plants; the third, that from year to year the climate deviates widely from the normal. A certain flora may adapt itself to grow in a given spot, but may be exterminated by several unusually severe summers, after it has been established for several years. Shortage of water, and particularly shortage at seasons when the plant's requirements are large, is a most important factor

in the production of deserts, but is by no means the only factor, and under certain circumstances places can be utter desert in spite of receiving a liberal and not ill-distributed supply of water.

iii. Heat

The temperature is of fundamental importance to the flora and fauna, not only for its own sake, but because it influences the humidity of the air and the evaporation of moisture. It is generally realized that the climate of a desert may be intensely hot; it is equally true, though not so well known, that it may be extremely cold. Considerable daily and yearly range of temperature is a characteristic of the climate of all great land areas, and we are justified in presuming that the extremes of temperatures of the desert are partly due to the fact that most desert areas lie in the centre of large land masses. This presumption is supported by the fact, to which we shall return later, that desert areas which lie close to the sea are not subjected to extremes of heat and cold. But we must not attribute the range of the temperature exclusively to the continental position of deserts, because the extremes encountered in deserts are much greater than they are in other continental areas; and we believe that the very great fluctuations of temperature are due very largely to the bareness of the soil and the clearness of the sky. The radiant heat of the sun is not impeded either by cloud or by vegetation from striking directly on the soil, which is

warmed very rapidly to a high temperature. The hot surface of the earth then warms the lower layers of the atmosphere by conduction, and produces high air temperatures. At night, on the other hand, there is no blanket of vegetation to hinder loss of heat from the ground. Therefore much of the heat which has accumulated during the day in the

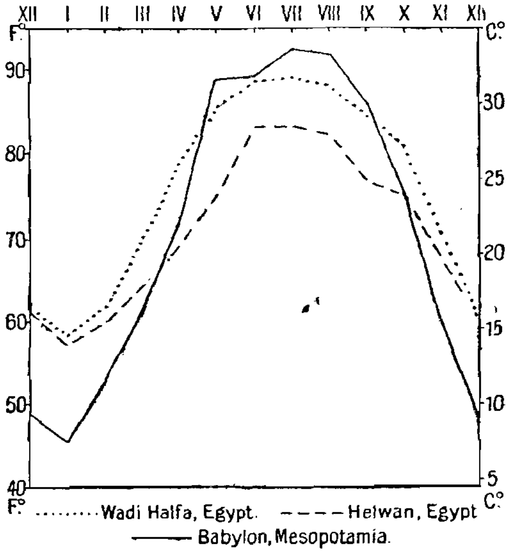


Fig. 4.—Average Monthly Mean Shade Temperatures of Three Places in the Great Palæarctic Desert.

superficial layers of the soil is radiated into space between sunset and sunrise.

The monthly average temperatures of certain desert stations are shown graphically in Fig. 4. Two things are apparent: very high temperatures are attained in deserts, higher in fact than are ever reached in many places closer to the Equator, and very wide annual ranges of temperature are char-

acteristic. Almost any place in any desert will show these essential characteristics of the desert climate, provided it is not close to the sea.

The contrast between a hot summer and a cold winter is shown not only by mean figures, such as those on which Fig. 5 is based, but even better by quoting the extremes of temperature which have been recorded at a given spot either in one year or in a series of years. The following are good examples:

Place.	Period	Absolute Range.	
		° C.	° F.
Mosul, Mesopotamia	7 years	66·5	119
Baghdad, Mesopotamia . . .	28 ,,	57·8	104
Petroalexandrovsk, Turkestan .	10 ,,	71·8	128
Tashkent, Turkestan . . .	10 ,,	70·2	126
Ghardaia, Algeria	1 year	57	102
Kasalinsk, Turkestan . . .	1 ,,	88	158

The following figures from Wadi Halfa (Anglo-Egyptian Sudan) are interesting because they show that though the normal range of temperature is great the occasional range is very much greater: the coldest month is January, with a mean lowest reading of 7·8° C. (46° F.); the absolute lowest reading in twenty-one years was −2·2° C. (28° F.); the mean highest reading is 41·1° C. (106° F.) (June), the absolute highest being 52·5° C. (130° F.) in April. It is clear that a slight frost, occurring once in a score of years, at a place in which the thermometer does not pass below 7·8° C.

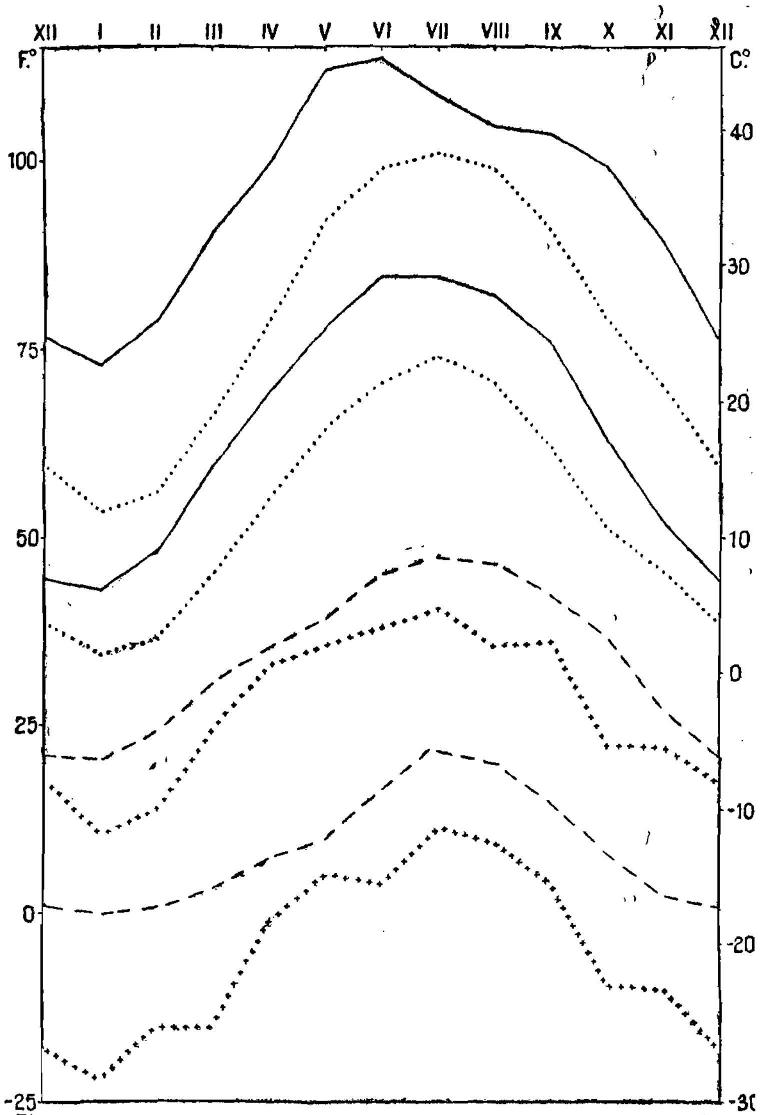


Fig. 5.—Monthly Mean Maximum and Mean Minimum Shade Temperatures of Four Places in the Great Palæarctic Desert

(46° F.) in an average year, might devastate the flora.

The daily range of temperature is scarcely less striking than the yearly, and is characteristic of all desert areas except those in close proximity to the sea. Cannon quotes figures which show that the extreme daily range of temperature recorded during three years at In Salah and Wargla in the Algerian Sahara is about 36–40° F. (20–22° C.) in the winter months and about 50–52° F. (28–29° C.) in the summer months. The average range of temperature on a single day in Baghdad, Mesopotamia, is 21° F. (11·7° C.) in January and December, and 31° F. (17·2° C.) in August and September. But though the daily fluctuation of temperature is generally highest during the hot months it appears that the greatest range which has ever been recorded in a single day was observed in December at Bir Milgha in Southern Tripoli by Rohlfs: he recorded a range of 68° F. (37·8° C.), from 31° F. to 99° F. (– 0·5° C. to 37·2° C.), within twenty-four hours.

Many other instances of extremely rapid change of temperature are on record: Paulsen observed the shade temperature to be 37°, 68°, and 82° F. (3°, 20°, and 28° C.), at 6 a.m., 9 a.m., and 1 p.m. in sand desert in Transcaspia. He also records the following figures at Tachta, on the Murgab River, on the 23rd of June:

6 a.m. Shade temperature 78° F. (25·5° C.). Sun temperature 93° F. (34·0° C.)
8 a.m. Shade temperature 85° F. (29·5° C.).

11 a.m. Shade temperature 104° F. (40·0° C.). Sun temperature 122° F. (50° C.)
3 p.m. Shade temperature 109° F. (43·0° C.). Sun temperature 129° F. (54° C.)

It will be noticed that enormous fluctuations in the temperature of the day, and of the year, are generally recorded from such places as Kasalinsk, Petroalexandrovsk, and Tashkent, in which the effect of desert conditions is reinforced by a position in the centre of a great land mass. On the other hand, certain places which are close to the sea are not liable to extremes of temperature, but are veritable deserts. Fig. 6 shows the monthly average maximum and minimum temperatures of El Arish, Aden, and Bahrein, all of which are in desert areas, on the coast of the sea. One concludes that great daily and annual range of temperature is a common element of desert climates, but not an essential characteristic. The bright sun shining unimpeded on the desert soil heats it very rapidly, so that by midday the temperature of its surface greatly exceeds that of the air above it.

Our knowledge of the temperature reached by the surface of the soil is slight, but I hope shortly to publish records which show that in summer in South Palestine the surface of clay desert rises about 36° F. (20° C.) beyond the shade temperature at midday. Nearer the Equator no doubt even higher readings would be secured, but in Palestine surface readings of 122–140° F. (50–60° C.) are normal. Prezhevalsky has recorded similar figures for the

may be as cold as $-16°$ F. ($-26·5°$ C.) in winter. The highest readings which have so far been taken of the surface of the soil were taken on bare sand; e.g. readings of 183° F. (84° C.) on the Loango Coast, close to the Equator, and Augièras' record of 172° F. (78° C.) on a sand dune in the Sahara. The surface soil reaches such a high temperature by day

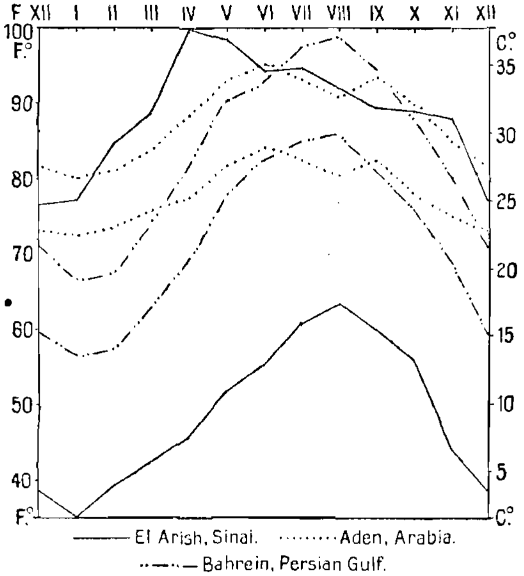


Fig. 6.—Monthly Mean Maximum and Mean Minimum Shade Temperatures of Three Places situated on the Sea Coast of the Great Palæarctic Desert.

that it does not cool completely during the ensuing night: as a result the minimum temperature reached by the surface of unshaded soil at night may be several degrees above the minimum temperature of the air (C. B. Williams). It is only the superficial layer of the soil which is liable to these great fluctuations of temperature.

At Tucson, Arizona, in June, the temperature ranges daily through about 17° F. (10° C.) at a depth of 6 inches (15 cm.) in the soil, and over about 2° F. (1° C.) at a depth of 10 inches (25 cm.); at the same season the shade temperature ranges over about 57° F. (37° C.). Therefore at 6 inches (15 cm.) the daily fluctuation is about one-quarter of that of the air, and at 10 inches (25 cm.) it is only about one-thirtieth. Results which are essentially similar have recently been obtained by C. B. Williams in the desert near Cairo, Egypt, in July. The same investigator sends me the following data taken in April, 1922, at Luxor, Egypt, on cotton land which had been irrigated three weeks previously: air temperature 86° F. (30° C.), soil surface 131° F. (55° C.), soil at 3 inches (7·5 cm.), 81° F. (27° C.); at the same time the relative humidity of the air was about 15 per cent., and the relative humidity 3 inches deep in the soil 98 per cent. These observations may be taken as typical of others which have been made in South Algeria and other deserts. It will be seen that an animal would very easily reach equable conditions by burrowing, and that it would pass through a very great range of temperature and humidity as it entered or left its burrow during the middle of the day.

iv. Relative Humidity

The rainfall and the temperature of the desert have been discussed: upon their interaction depends the relative humidity of the air. It is defined as the amount of water-vapour which the air contains com-

pared with the amount which it would contain if it were saturated with moisture from a flat surface of water at the same temperature. Relative humidity might, of course, be expressed as a vulgar fraction ; we could say that it was " one-third," meaning that the air contained a third of the amount of water-vapour which it could hold if saturated at the particular temperature under discussion. But it is generally more convenient to express the humidity in percentages, the figure 100 representing saturation. The amount of water-vapour which the air can hold varies very greatly with the temperature, and it rises constantly as the temperature rises, so that a much greater amount of water-vapour is required to saturate a certain volume of air when it is warm than when it is cold. Suppose, for instance, that the air is saturated with water-vapour in the cold early morning, and that the actual amount of moisture in the air remains constant throughout the day : then the relative humidity will fall steadily as the temperature rises, because the air when warm could contain much more moisture than it actually does contain.

This is what happens in most parts of the world on most days in the year. Among masses of dense vegetation and in damp places it is hardly noticeable because, however warm the air becomes at midday, it can still saturate itself from the wet soil and the vegetation. But in deserts the difference between midday with its low relative humidity, and the night with its high relative humidity, is extremely pronounced, because, as we shall see later, fluctuations

of temperature are excessive, and there is little moisture available to increase the humidity of the air when its temperature rises. There is, therefore, a great contrast between the forest type of climate, with a very constant humidity, and the desert type, in which the humidity fluctuates widely in each period of twenty-four hours.

In point of fact such a range of relative humidity

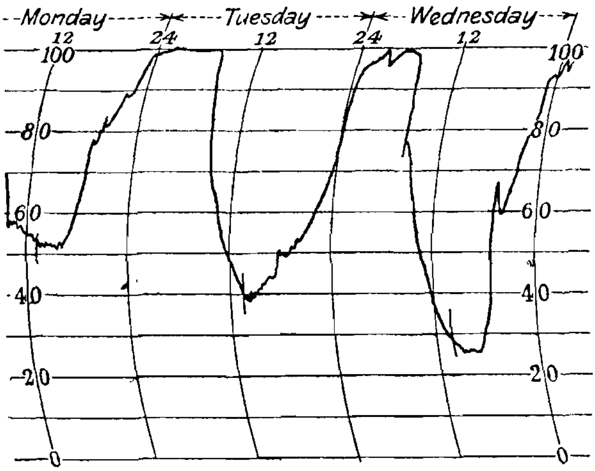


Fig. 7.—Curve obtained from Recording Instrument showing Daily Fluctuation in Relative Humidity at Gizeh, Egypt, 20th–22nd March, 1922.

The figures on the side of the graph represent percentages of humidity. (C. B. Williams.)

as is shown in Fig. 7 does not occur from one year's end to another in many tropical forests, yet at Gizeh, Egypt, it is a normal daily occurrence during the summer. The curve of which Fig. 7 is a reproduction was actually made during the end of March, 1922, and shows that the humidity can drop from saturation to 20 per cent. in a few hours. Fig. 8, which shows the daily fluctuation (8 a.m. and 4 p.m.)

of relative humidity at Mosul, Northern Mesopotamia, during an average week in June and an average week in December, shows this point equally clearly. Very similar figures are obtained if the

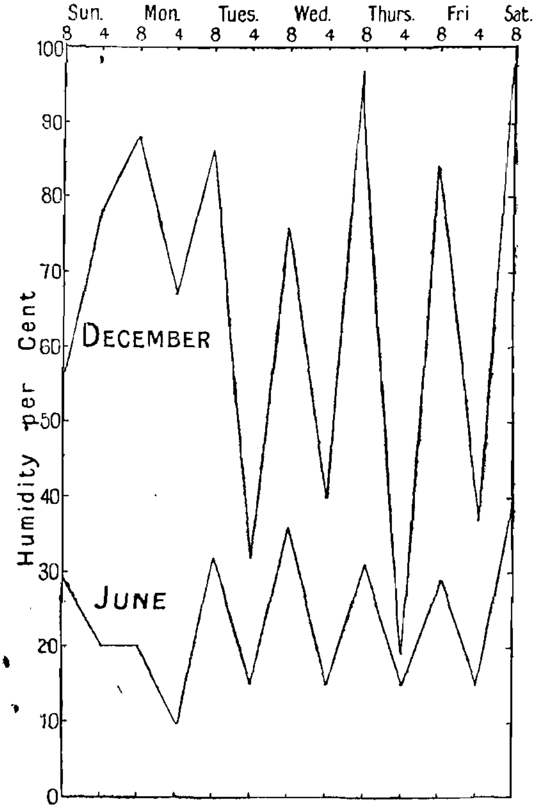


Fig. 8.—Relative Humidity at Mosul, N. Mesopotamia, at 8 a.m. and 4 p.m. during an Average Week in June and an Average Week in December.

mean of a series of readings is taken. Fig. 9 represents the mean relative humidity taken at intervals of two hours every day from June to September, at Mohammerah, near Basra. The daily fluctuation in the humidity is, of course, less striking because

this figure is based on average readings for that period, and the fluctuation would be even more remarkable were figures available, not from Mohammerah itself, which is on the Karun River among date palms, but from a spot two or three miles from it in bare desert country.

Relative humidity varies very greatly within very short distances. Observations taken among a few palms, or in a cave or house, show a humidity very much less variable and generally higher than

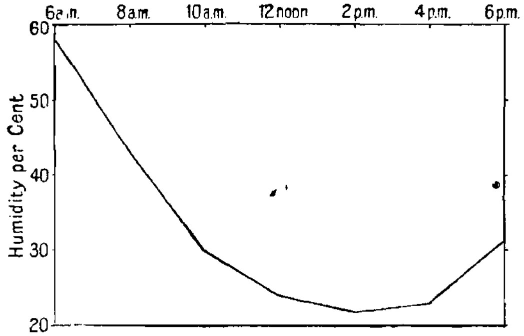


Fig. 9.—Mean Relative Humidity at Two-hourly Intervals for the Months June, July, August, and September at Mohammerah, Persian Mesopotamia.

that which is prevailing a few yards away in open desert.

It is generally true that the greatest fluctuations in relative humidity occur during summer, and this depends largely on the fact that the temperature fluctuates more during a summer day than a winter day (page 19). Rapid and wide alterations in the relative humidity are therefore one of the many climatic factors which combine to attack both plants and animals in summer, in deserts.

The ordinary statistics of relative humidity published by official meteorologists are very unsatisfactory for the biologist. In many places readings are only taken in the morning and evening, and the full stress of extremely low humidity which oppresses the flora and fauna at midday passes unrecorded. Furthermore, readings are often taken at a place convenient to the observer, seldom out in the desert, and the readings of humidity suffer perhaps more than any others because of the variations which occur between places a few yards inside or outside an oasis. It is also to be remarked that readings are sometimes taken at 8 a.m. and 8 p.m., the two times at which the humidity is changing most rapidly. If, therefore, the reading is taken a few minutes too soon or too late a considerable error may be produced.

v. Wind

Rapid fluctuation in the temperature of the surface of the desert, and of the air above it, results in air-currents, which are generally greater in summer than in winter. At any rate, in the Great Palæarctic Desert a calm during the middle of the day is rare, and in many places winds of constant direction are experienced at this season. The sirocco is a hot easterly or southerly wind which blows in Palestine, Algeria, and other parts of the Mediterranean littoral; the shamal, in Mesopotamia, blows from the north-west for many days at intervals all through the summer. During June, July, and August, which

are the windiest months of the year, 75 per cent. of the wind, and an even higher proportion of the stronger winds, are from this quarter. The sirocco and the shamal are two examples of the strong winds from a certain quarter, which blow with regularity in many deserts, but other and more violent regular winds are on record.

At Menjil in North-West Persia a wind of great violence and regular occurrence blows whenever the sun is shining brightly on the Persian plateau. It is caused by the rising of the air which has been warmed by the hot plateau, and the consequent inrush of unwarmed air from the surrounding areas. At Menjil this is concentrated in the gorge of the Safid Rud, a river which here cuts its way through the Elburz Mountains, and a constant violent wind blows through the gorge all the day long, throughout the summer. This wind is of such strength that one can only walk against it with the greatest difficulty, and I have seen a loaded camel entirely unable to make headway against it; tents can only be pitched during the hours of relative calm in early morning and late evening, and when securely pitched are generally ripped to shreds. Even more violent winds have been experienced in many desert areas, but few of them are of such regular occurrence as the Menjil wind. Augièras, for example, has recorded that in February, 1915, a violent wind kept him prisoner under the lee of a rock at Erg Chech in the Western Sahara for no less than nine days, and a month later he experienced a gale which carried a camel saddle 200 metres. The effect of wind-driven

sand upon rock is illustrated in Fig. 11 (facing p. 42).

The hot air which rises from contact with the heated desert sometimes makes its way upwards in vortices, or dust-devils. The dust-devil is a rotating column of air, and is generally seen on very hot days on which a moderate breeze is blowing. It is very sharply delimited, and owing to its load of debris, dust, and bushes, it is easily visible. It moves slowly about in the desert, following the direction of the wind rather irregularly. The height of the vortex is variable; a century ago Lane measured one of 750 feet in Egypt and saw others taller, but the majority were shorter; they were continuous columns reaching up from the ground for several hundreds of feet. Normand observed dust-devils at Samarrah in Northern Mesopotamia, some of which were at least 300 metres high, though only about 5 metres wide at the base. Sometimes these vortices lose contact with the ground, but maintain their existence at very great heights. Flying officers in Mesopotamia have encountered vortices of this sort whirling upwards at a height of 5,000 feet above the ground and still carrying dust and debris. Even a very small dust-devil is violent; I have had my shirt stripped from my back by a vortex which seemed to be only a dozen feet in diameter, and during the operations in Mesopotamia and North-West Persia it was no uncommon sight to see a particular tent struck and emptied of its contents by a small vortex, which left untouched other tents only a few yards away. Larger vortices are much

more devastating ; in 1918 a very large camp at Balad Ruz, north-east of Baghdad, was struck by a dust-devil of unusual size, which carved its way through the camp, leaving a lane in which not a single tent was standing. Heavy articles of kit were blown as much as 200 yards through the air, and an officer of my acquaintance was scooped out of his tent with all his camp furniture, and dropped twice, the second time with several broken ribs.

The effect of wind on other climatic conditions is various. A hot dry wind causes a rapid and considerable drop in the relative humidity, and generally a rise in temperature. Often, however, the wind causes a drop in temperature, because it mixes the lower layers of the atmosphere, which have been heated by contact with the hot earth, with the higher layers which have not been so heated. A wind heavily laden with sand or dust, and blowing for many hours on end, may cause a most marked drop in the day's temperature, by shielding the land from direct sunlight.

vi. Evaporation

Though on one hand the rainfall is meagre, on the other the evaporation is excessive in all deserts and at nearly all seasons. The rapidity with which water evaporates, whether from the superficial layers of the soil or from hollows in which it has accumulated, is caused by the high diurnal temperatures, by the direct rays of the sun beating down from a cloudless sky on bare earth unprotected by a covering of vegetation, and by the unimpeded action of the

wind.' Figures are available from a limited number of desert stations giving the number of inches of water which would be evaporated from an open surface of water by the month or by the year. These figures do not represent what actually happens in the desert, because very soon after a fall of rain the surface of the soil is dried and evaporation practically ceases. But if they are taken in conjunction with the figures for annual mean rainfall they represent very vividly the discrepancy between the water upon which the plants can draw and the desiccating effect of the desert climate and sun. This ratio between possible evaporation (*e*) and actual rainfall (*r*) is of very great interest to biologists, and it is probably one of the most important factors in determining whether a place will or will not be desert. So far as we know it is high in all desert regions, and it is not high in regions which are not desert.

The following examples show the very high possible evaporation in deserts, and the ratio between this and the actual rainfall:

Place.	Rainfall (Mean), Inches (*r*).	Evaporation, Inches (*e*).	*e*/*r*.
Yuma, Arizona	3·26	100	30·7
Piute Dam, Utah	8·61	61·2	7·1
Tucson, Arizona	11·58	90	7·8
Mohave	4·97	95	19·1
Cahuilla, California	17·35	116	6·7

Cannon has given the following figures, which show that at Laghwat and Ghardaia the discrepancy

between rainfall received and possible evaporation is immensely and irregularly increased in the summer and autumn months, the very period when the other

Table showing the ratio between evaporation and rainfall month by month in 1908, at two stations in the Algerian coastal zone and two in the Algerian Sahara. Evaporation has been calculated as from a free water surface. Readings from a Piche evaporimeter have been corrected.

	Jan.	Feb.	Mar.	Apr.	May.	June.	July.	Aug.	Sep.	Oct.	Nov.	Dec.
Oran . .	1·3	1·9	1·6	1·3	17·4	8·5	59	146	18	2·45	3·4	4·4
Algiers . .	0·6	1·3	0·5	1·1	22·3	11·7	219	28·8	5·0	1·0	1·2	1·1
Laghwat .	3·1	4·7	9·8	203	7	373	421	21	25·9	14·2	154	104
Ghardaia .	8·9	233	81·4	529	38·9	699	166	25·6	66·9	23·2	49·7	225

forces of nature all combine to make life impossible for any plant or animal except those specialized for life in a desert. The ratio is lower and less fluctuating in the coastal non-desert stations (Algiers and Oran). Cannon states that if the annual evaporation-rainfall ratio of the littoral zone be taken as unity, that of the high plateau is 3·7 and that of the desert (average of Laghwat, Ghardaia, and El Wad) is 18·6.

It will also be appreciated that in an unusually dry year the evaporation-rainfall ratio will be vastly increased, so that, at a time when the mere drought is pressing hardly on the flora and fauna, an increased discrepancy between rainfall and evaporation is also thrown into the scale against them. If, for instance, the normal evaporation-rainfall ratio for Mohave, with a mean rainfall of 4·97 inches (125 mm.) is 19·1, then in the dry year with a rainfall of only 2·20 inches (55 mm.) the ratio would be 43·2, if we

suppose that the evaporation in that particular year was average. Judge, then, how great must be the fluctuations in this important ratio in spots in the Libyan Desert where the rain falls only once in every four or five years, and where the evaporation is believed to be 150 inches or over.

vii. Light

The uninterrupted sunlight of Egypt, even in the winter months, is a thing which has arrested the attention of every tourist. Accurate records of the intensity of sunlight in deserts are scarce, but one can at any rate recall a few general truths. The sun's rays consist not only of light rays and heat rays, but also of ultra-violet and other rays which are known to exercise very definite influences on living matter. All these rays, but particularly the ultra-violet rays, pass more readily through dry than through damp air; their effect on plants and animals is therefore much more potent in summer than in winter, for in summer the days are longest, the sun most nearly vertical at midday, clouds are absent, and the amount of water-vapour in the air at its lowest.

viii. Summary

We have discussed individual elements of the climate; let us now try to consider the climate as a whole, built up of these and other component elements. If we were to study only the average meteorological statistics for a number of places in the Great Palæarctic Desert we should realize at

once the great contrast between the summer and the winter. The summer is rainless; it is very hot by day but much cooler at night, and the relative humidity of the air varies very greatly in the twenty-four hours; the daily fluctuation in the temperature of the air is exceeded by that of the temperature of the surface of the soil; the sky is clear, the day long, the atmosphere dry, and the sun vertical or nearly so at midday, and it follows that the effects of the sun's heat and chemical rays are very great; the winds are strong and constant in direction, and occasionally violent and destructive; evaporation is extremely active and far exceeds the amount of moisture received by the soil. In every respect the climate in winter is different from that in summer. It is information of this sort which we shall glean from mean statistics, but they only tell us a part, and an unimportant part, of the truth. It is not the contrast between the seasons, immense though it is, which is the essential character of the desert climate.

Rather it is the extraordinary deviations from the mean which mark out the desert climate as a thing quite distinct. It is to the maximum and minimum figures, not to the means, which we must look if we are fully to realize the difficulties with which desert plants and desert animals have to contend. It is not the regular succession of summer and winter, however dissimilar, but the occurrence of long droughts, torrential rains, unusual frosts, violent whirlwinds, and other irregular phenomena

that have prevented the covering of the ground with vegetation and the peopling of the vegetation with a normal fauna. It is also to be constantly remembered that many different factors go to determine that land shall be desert: here it is drought, there it is wind; in other places, as we shall see in the next chapter, it may be shifting sand, or salinity of the soil, or absence of drainage or of humus.

CHAPTER II

THE SOIL AND WATERCOURSES

The physical environment of a creature includes not only the climate of its habitat, but also certain factors which may collectively be termed "geological." Among them are the type of soil on which it lives, the flatness or hilliness of the country, and its exposure to or protection from sun, wind, and rain, and the existence of supplies of water other than rain and dew.

The influence of the geological environment upon the desert plants and animals is almost as important as the influence of climate, though less attention has been given to it. The prevalent notion that deserts are uniform stretches of sand dune is entirely erroneous, for desert soils exhibit a wide range of chemical and of physical characters. The soil of a desert is commonly gravel, or sand, or bare rock, or sunbaked mud; other types of soil are found, and almost the only soils which never occur are those which result from the presence of plentiful vegetation, for instance loam and peat. The scarcity of humus is probably an important factor tending to prohibit all but a few specialized plants from colonizing deserts; in fact this, and the general

badness of the drainage, are common characteristics of desert soil.

It is to be remembered that various types of desert pass gradually into one another. Clay desert passes by insensible steps through clay desert containing a few stones to stony desert; at the other end of the scale stony desert may contain so many large stones and so little fine soil that it is not far removed from rock desert. Further, an area which is uniform so far as soil is concerned may be bare desert in one place, semi-desert or steppe in another, by reason of the presence of windbreaks, or of different exposure, or of other factors. One cannot draw sharp lines of delimitation between the different types of desert, nor between areas which are desert and others which are semi-desert. The limits of a desert are indefinite not only in point of space; they vary also with time. This is so characteristic a feature, and so striking when one has actually seen it, that I shall return to it again and merely state in passing that bare earth tenanted by a few specialized plants and animals and exposed to the full rigour of a desert summer may enjoy a delightful spring during which it is carpeted with lush, unspecialized flowering plants and teeming with bees and butterflies. For two or three months one may truly say that the desert has vanished (Figs. 24, 25, facing p. 58).

It is impossible to understand the relationships between the soil of a desert and its flora and fauna without understanding the powers which are possessed by all soils, in varying degrees, of holding

water, of allowing it to sink through them, and of raising it from lower levels by capillarity. In general we may say that evaporation of water from the surface of the desert soil is due to the heat of the sun, the movement and dryness of the air, and the nakedness of the earth. Evaporation (page 30) exceeds rainfall in deserts, except in very short periods in the year: therefore the surface of the soil is normally quite dry. But at short distances beneath the surface one frequently finds a proportion of moisture which is surprising, and the proportion rapidly increases at slightly greater depths: it is impossible in a general discussion to quote figures, and the depth varies with such factors as type of soil, interval since last rainfall, and the depth of the permanent moisture in the soil. The explanation of the dryness of the surface and dampness of the deeper soil is that after the soil has been saturated by a fall of rain the surface rapidly dries: this drying process penetrates to greater and greater depths, becoming slower and slower, because the action of wind is cut off, and the diffusion of the damped air is retarded by the superficial layer of soil which is already air-dry. There is continual upward movement of moisture from the depths of the soil in which water was accumulated when the rain fell, and to which in certain cases water is brought by seepage from springs, rivers, or water-bearing strata. This upward movement depends on capillary attraction, which enables the water to rise above the level at which it would naturally lie, by

penetrating the minute spaces between the soil particles. There is then an upward movement of water, from the subsoil, due to the capillarity, and a downward movement of the level from which evaporation is taking place in the soil. This downward movement is slower the farther from the surface it is taking place: at a certain point the upward and downward movements balance one another, and at this level the moisture in the desert soil remains constant, unless equilibrium is upset by fresh rainfall or increased evaporative power of the air, or some other disturbing factor. These facts have a practical application. Cultivation of arid land is sometimes rendered possible by the employment of a machine which reduces the surface of the ground to fine powder (" dust-mulch "). This layer of fine powder, penetrated by correspondingly minute air-spaces, decreases the upward diffusion of the air which has saturated itself with moisture in the soil. The decreased upward diffusion results in decreased evaporation, and equilibrium is disturbed, to be re-established nearer the surface, at a point where the upward movement of the moisture once again balances the lessened evaporation. But as the moisture in the soil now lies at a higher level it is possible to plant and raise crops which could not have come to maturity without the aid of the " dust-mulch " (Livingstone).

Bearing it in mind, then, that terms such as " sand desert," " gravel desert," are not capable of exact definition, or of exact geographical delimitation, let us turn our attention to some of the

commoner different types of soil of which the desert may consist, and the various problems which have to be faced by organisms which inhabit the sand, or gravel, or rock, or mud.

The sand is in many ways the most hostile of all environments. Its surface is very smooth, and offers little impediment to the wind. As has been said already, winds in any desert tend to be strong, sometimes violent: in sandy desert their action is unchecked by any obstacle. These winds are detrimental to the plants; they break leaves and branches, they greatly increase evaporation from the soil and transpiration from the plant, and they carry abrasive particles of sand and soil.

As the surface of most sandy areas is frequently in motion, even in the absence of sand-storms, it is extremely difficult for plants to colonize them. Young seedlings are overwhelmed, tender shoots are damaged by blown sand, and roots are laid bare to the sun. In certain places where the surface of dunes is particularly unstable no vegetation of any sort grows. In the Indian deserts, according to Blatter and Halberg, the fairly copious monsoon rains may temporarily consolidate the surface of a dune which at other seasons is unstable. Seedlings of various plants then spring up and, as the sand dries, some individuals of certain species hold their own, while the rest die. In all parts of the world spots which are less wind-swept are colonized by special plants, many of them grasses, which resemble the marram of our own coasts in their habit, and after they have established themselves and to

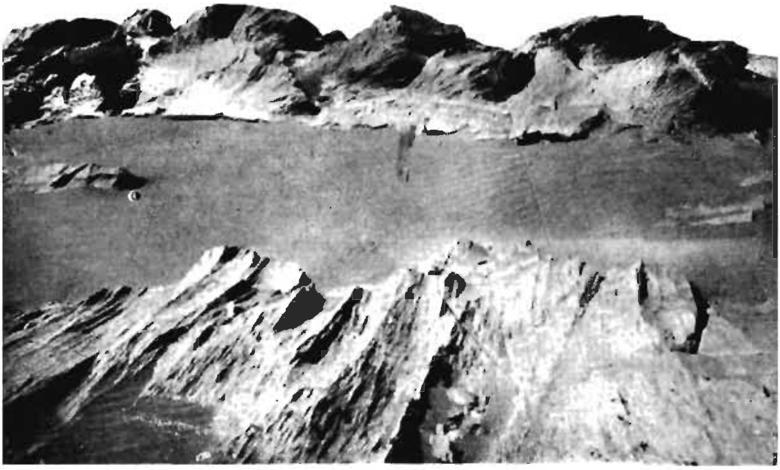
some extent consolidated the dune, a number of other plants are able to take root. These all tend to hold together the sand around their roots and to protect the surface of the dune from the wind and from evaporation. There is therefore a tendency for the dune to become more and more solidified and immobile, and more and more covered by vegetation: each plant that grows and then dies increases by a little the organic constituents of the dune, and by that much decreases one of the factors which render colonization of its surface so difficult.

The relationships of sand to rain falling on it are remarkable. Water which falls on its surface sinks in with extreme rapidity, and to a considerable depth: and the tendency for the water to rise by capillarity is slight, because the sand-particles are relatively large. Therefore the rain which falls on sand is of no use to short-rooted plants. On the other hand, as it sinks rapidly and as the surface of the water remains at a considerable depth, loss by evaporation is less than in any other type of desert. In fact, the sand dune is a sponge, and most of the water which it receives it holds. The conditions favour long-rooted perennials rather than other types of plant. The sparse flora of a sand dune in the Great Palæarctic Desert often consists solely of perennial grasses and deeply rooted switch bushes, but in parts of Transcaspia, where sand overlies impervious loess at no great depth, quite luxuriant vegetation grows even in summer (Paulsen).

In places where sand overlies an impervious rock, copious water is available for the cultivation of deep-rooted plants, which flourish when once they are established. Just to the south of Jaffa, in Palestine, is a large area of shifting dunes, with a sparse flora and fauna, closely adapted to their environment. The land was in fact indubitable desert until certain astute people discovered that vines would grow luxuriantly in depressions among the dunes. In these places water can be obtained at all seasons by sinking wells to about 6–8 feet, and when once the young vines are established they grow well and produce grapes in the dry, hot autumn, at a time when the dunes appear a little more dry and barren than usual.

Another plant which grows well in deep sand is the date palm. Its root system attains a remarkable length while the plant is still young and small, and reaches deep-lying supplies of water. Hartert and other travellers have described the conditions of date culture at El Wed in the Algerian Sahara (Figs. 10 and 12). The town and gardens are in imminent danger of being overwhelmed by moving dunes, and are constantly afflicted by violent sandstorms. Subsoil water is plentiful at a considerable depth in the sand, and the inhabitants excavate large pits in the sand, and at the bottom plant offsets of palms. At first watering by hand is necessary, but after a few months the young palm's roots reach the subsoil water : the owner's task then is to remove the sand which threatens to cover his trees, and at this task he labours almost un-

g. 10.—Date Palms Growing in Artificial Depressions in Sand Dunes at El Wad, S. Algeria. (*Photo:* V. H. W. Dowson. July, 1922.)



g. 11.—Ridge of Cretaceous Limestone carved by Wind-driven Sand. at Umm Shersher. S. of Kharga Oasis. Libya. (*Photo:* F. W. Green. Geol. Survey. of Egypt.)

g. 10.—Date Palms Growing in Artificial Depressions in Sand Dunes at El Wad, S. Algeria. (*Photo:* V. H. W. Dowson. July, 1922.)

g. 11.—Ridge of Cretaceous Limestone carved by Wind-driven Sand, at Umm Shersher, S. of Kharga Oasis, Libya. (*Photo:* F. W. Green, Geol. Survey. of Egypt.)

ceasingly with his basket; he also dusts his vegetables with a small brush to free them from drifted sand. Figs. 10 and 12 show clearly the contrast between the flourishing palm which has tapped the subsoil water, and the barren dunes which surround it. The palm-leaves inserted in the sand in Fig. 12 are intended to check wind-driven sand: there is no undergrowth because the water supply is so deep.

The Nefud, or areas of sand dune in Arabia, are relatively fertile and support so much indigenous vegetation that they are recognized winter and spring pastures. Camels grazing in the Nefud in spring are able to dispense with drinking for long periods. Doughty records that the inhabitants planted a dune at Boreida with tamarisks, and that after one year the trees were established and no longer in need of artificial watering.

Sand deserts of various types may be distinguished: bare, shifting dunes, more stable dunes covered with plants, and undulating plains. In the desert west of the Nile, and in many other places, areas of loose sand alternate with outcrops of rock, and the rock is often etched and carved with fantastic shapes by the wind-driven sand grains (Fig. 11). Sand desert of one kind or another is said by Cana to occupy 700,000 square miles of the Sahara, an area equal to about one-fifth of the whole; according to Augièras, dunes up to 200 metres in height exist in the Western Sahara: no other area of equal extent is known. The Takla Makan, in Eastern Turkestan, is a sandy

Fig. 12. Date Palm growing in a Pit at El Wad, S. Algeria. (*Photo:* V. H. W. Dowson. July, 1922.)

Fig. 13. —Expanse of Salt Mud at the North End of the Dead Sea, Palestine. (*Photo:* P. A. Buxton.)

Fig. 12. Date Palm growing in a Pit at El Wad, S. Algeria. (*Photo:* V. H W. Dowson. July, 1922.)

Fig. 13.—Expanse of Salt Mud at the North End of the Dead Sea, Palestine. (*Photo:* P. A. Buxton.)

and so consolidated, there is no subsoil drainage. One finds therefore that some degree of saltness is characteristic of flat clay or mud deserts. In the parts which lie a little higher than the rest, and from which the salt is washed by the rain, the salinity is slight, and plants, many of them specially adapted to growth in salt places, may be found. In the depressions it is common to find an incrustation of crystals of salts, and an absence of vegetation of any kind whatsoever (Fig. 14), or one may find that the ground is slimy, even in dry weather, owing to the hygroscopic properties of the salts which it contains. Around the margins of these salt patches one finds an intermediate zone inhabited by salt-loving plants, such as grow at home on sea marshes. In Fig. 14 the plants on the right are Suæda: they are growing on land which is a few inches higher than that on the left, which is covered with white salt-crystals. Fig. 15 shows *Atriplex halimus* and other bushes which love salt, growing on a plain of salt mud.

The salts found in these positions vary. Common salt (sodium chloride) is, I believe, always present, but in less proportionate amounts than in sea water. In Transcaspia magnesium and sodium sulphate are common, and calcium sulphate (gypsum) occurs. In Mesopotamia different proportions of chlorides and sulphates of sodium, calcium, and magnesium all occur in relatively large quantities, in the salt and alkaline lands.

Figs. 16 and 17 show a peculiar type of salt clay desert which is found at the lower end of the

Jordan Valley, and in certain spots round the margin of the Dead Sea. The soil here is so impregnated with salts that in spite of an annual rainfall of 16–18 inches, and in spite of the excellent surface drainage provided by these slopes, no vegetation exists. My friend, Mr. Raczkowski, of the Department of Agriculture, Palestine, made an analysis for me of the surface soil of one of the hillocks shown in the plate; the analysis was made in February, just after the winter rains which one might suppose would have washed much of the salt *out of the superficial layer of soil.* Nevertheless, the analysis revealed the presence of 0·58 per cent of sodium sulphate, 0·57 per cent of sodium chloride, and 36·13 per cent of sodium carbonate. Any one of these salts in such high proportions would be sufficient to prevent the growth of plants, except forms specially adapted to exist on salt soils: their united effect is to render these clay hills absolutely devoid of plant life at all seasons of the year.

The loess of Transcaspia and Turkestan and the fine silt of the plains of Lower Mesopotamia are very fertile if they are irrigated and if provision is made for the removal of the water after it has flowed upon the land, so that mineral salts do not accumulate unduly. In Southern Mesopotamia the rainfall is not inadequate, and combined with the annual flooding from the Tigris and Euphrates would be sufficient to sustain considerable vegetation, were it not for the physical peculiarities of fine silt. Here, in fact, we have country which

Fig. 14.—SALT PATCH IN LOWER MESOPOTAMIA. (*Photo :* V. H. W. DOWSON.)

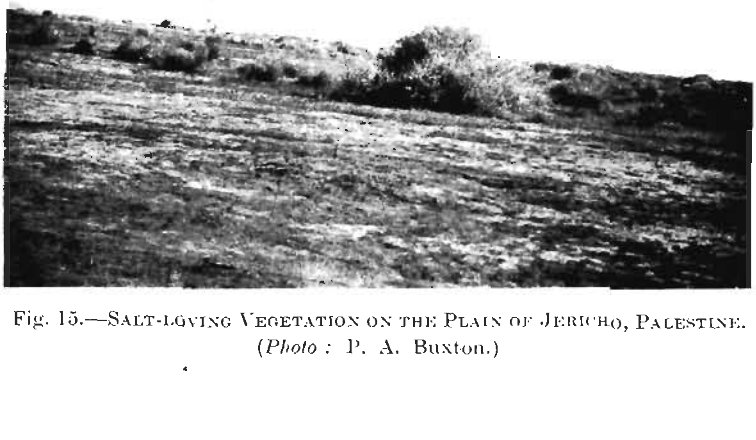


Fig. 15.—SALT-LOVING VEGETATION ON THE PLAIN OF JERICHO, PALESTINE.
(*Photo :* P. A. Buxton.)

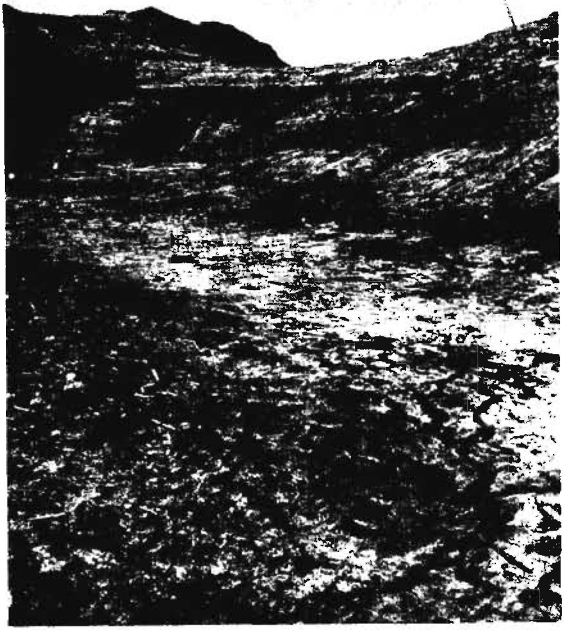
is desert, not because of its climate, but because of the physical characters of its soil.

The fact that smooth, hard deserts of silt or clay or loess support a very small fauna is partly due to the small number of plants occurring, but also to the fact that natural shelter from sun, drought, wind, and light is difficult to obtain. Even species which are capable of excavating burrows for themselves are liable to be drowned out by every storm of rain.

Very large areas of the Great Palæarctic Desert are composed of mixed stone and earth. This type of desert consists of varying proportions of stones, large and small, lying on and in clay or loess or fine earth of other kinds (Fig. 26). This mixed soil carries a relatively rich flora, if climatic conditions are not unfavourable. The finer element in the soil supports the flowers which it would naturally support if it occurred alone, and the presence of stones which hinder evaporation and by that means tend to conserve soil moisture, enables other plants to exist. In fact the mixed type of soil results in a rather varied flora, and this in turn increases the fauna. Apart altogether from their dependence on the plants, animals are more numerous in stony deserts because they find shelter from the climate under the stones. This point will be discussed later (pages 100–101). Stony desert, and semi-desert, is very widely distributed in the Palæarctic region, for instance in the Northern Sahara, the south of Sinai and Palestine, and large areas in Persia, Afghanistan, and Baluchistan.

Gravel desert, a type which consists apparently of pebbles with very little fine soil to fill up the interstices, has been described by Blatter and Halberg in Rajputana, and by Thomas on the edge of the Libyan Desert, north-west of Cairo. The intervals between the individual pebbles allow the immediate escape of any rain which falls; on the other hand, the surface of gravel desert is not liable to be moved by the wind. Gravel desert, as might be expected, supports a very poor flora: Thomas says that "standing in most places it is *impossible to see a single plant anywhere around* one. . . . At a period when the annuals have disappeared I have traversed several miles on patrols, without seeing a single plant." Though he studied his area during and after the spring rains he was only able to identify eight flowering plants in the gravel desert.

Outcrops of bare rock may occur in deserts of almost any type. Small areas of rock present intense difficulties to colonization by plants or animals: in any climate the plants growing on rock surface are rare, because soil is only found in small pockets (Fig. 18), and because nearly all the rain received runs off the rock at once: in deserts the difficulties are intensified. Larger areas of rock are less hostile to flora and fauna because they nearly always include patches of soil and little islands of plants. In most large areas of rock, caves occur, with their specialized fauna and relatively stable climate. A reference to the animals which are found in desert caves will be found on



Figs. 16 and 17.—Hills of Salt Mud near the Mouth of R. Jordan, nea Jericho, Palestine. (*Photo:* P. A. Buxton.)

page 104. In Fig. 18 I have illustrated a type of rock desert in which strata of hard and soft calcareous rock alternate. On the softer large numbers of spring flowers grow: these valleys are full of caves, both natural and artificial. Typical birds in this type of country in Southern Palestine are Rock Doves, Wheatears (*Saxicola lugens* and others), Rock Partridge (Alectoris = Caccabis), Ravens (*Corvus ruficollis*), and Tristram's Grackle (*Amydrus tristrami*): among mammals, Porcupines and the Coney or Hyrax (Procavia).

The influence of watercourses upon desert life is very much greater than might be supposed. Many of them are temporary, fed by snow, or by rain falling on some distant mountain mass, and run out into the desert plains, where they gradually disappear owing to evaporation and seepage into the soil. The length of such a river varies immensely with the season: at the end of a period of drought the whole bed may be dry (Figs. 19, 20, and 21); after a period of heavy rain a torrent may be produced sufficient to flow several hundred miles down a bed which has been dry for years. One of the longest of these dry watercourses is the Wadi Rummah, which rises near Medina in the highlands of Western Arabia, and at one time crossed the peninsula to discharge its waters into the Shatt al Arab near Basra. It is more than a thousand miles long, though its course is now blocked by large areas of sand dunes and water never runs from end to end of it. In some of these torrent-beds bushes and other vegetation grow (Figs. 20 and 21):

in others the floods are so violent, or the soil is so unfriendly, that nothing grows (Fig. 19).

These apparently dry beds form lines along which subterranean water drains, and in many of them it may be found by sinking a well to a depth of a few feet. This subsoil water determines the presence of a relatively dense vegetation (Fig. 21), consisting often of a fairly large number of species; these in turn provide food and shelter to very many animals. The bed of the stream gives life lavishly; as lavishly as it destroys it. A sudden heavy rainstorm, such as is common in deserts (page 13), falls, the water runs rapidly off the bare ground and produces a devastating flood. Shakespear saw such a flood as this in the Batin (lower part of Wadi Rummah) in Central Arabia; twenty minutes of heavy rain converted the dry bed into a rushing torrent 3 feet deep, 50 feet across. Such floods are not rare in Arabia. Philby has suggested that the desolation of the once populous Wadi Hanifa was due to a great flood which obliterated the settlements in the bed of the Wadi, and spared those on the sloping ground around; he records a flood in Wadi Dawasir which filled wells, and destroyed a hamlet, and another which drowned 150 men, 450 camels, and thousands of sheep, if local report is reliable. Palmer records a flood which destroyed forty bedawin and their flocks in the Wadi Solaf in Sinai, and doubtless examples might be multiplied.

Certain desert areas are traversed by great perennial rivers, such as the Tigris and Euphrates, the Nile, and the rivers of Transcaspia. In Lower

Fig. 18.—Wadi Nar, S.E. Palestine: Rock Desert. in which the strata of bare rock alternate with softer material. (*Photo:* P. A. Buxton.)

Fig. 19.—Sandy Bed of a Winter Torrent near Gaza, Palestine. (*Photo:* P. A. Buxton.)

Mesopotamia and the Nile Valley, and on the great plain through which pass the Amu Daria (Oxus) and Syr Daria (Jaxartes), plant and animal life depends less on local rainfall than on the annual flooding of the ground at the time when the river is at its highest. The height to which the river rises varies greatly from year to year, and depends on precipitation and the melting of snow in far-distant regions. The Nile is under partial control and the height of its annual rise is more constant than it would otherwise be: the Tigris is not under control, and the Euphrates only to a very slight extent. It follows that in a year of exceptionally high water great areas of Mesopotamia which would otherwise be unflooded are inundated in March and April and remain covered with water for several months. This not only keeps the soil of the plain moister than it would otherwise be in early summer, but materially modifies the summer heats, and appears to double or treble the number of insects which are on the wing throughout the whole summer. On the other hand, this annual flooding of a flat land is very unfavourable to the burrowing animals and appears to limit the species of lizards and small mammals very materially.

It is noteworthy that the majority of closed drainage basins, from which there is no outlet to the sea, are desert. This is probably due in the main to the fact that in them salts accumulate, until the increasing salinity of the area causes it to become desert. Examples are the great basins of Central China, Eastern Turkestan, and the Sahara,

into all of which rivers run from the surrounding uplands without ever making a sheet of water in the centre. Other closed basins, without outlet to the ocean but with inland seas or lakes into which they drain, are those of the Dead Sea and Jordan Valley; the Caspian with the Mugan Steppe and the steppes of the Volga and Transcaspia; the Sea of Aral with the Oxus and Jaxartes Rivers and the great plain of Russian Turkestan; the Shotts (Chotts) of Southern Algeria and Southern Tunisia; the Great Salt Lake in the State of Utah; Death Valley and the Salton Sea in California; and the Lake Eyre basin in Central Australia. All of these areas are desert, and the Dead Sea, the Caspian, the Sea of Aral, Death Valley, Salton Lake, and Lake Eyre are all beneath mean sea-level.

Fig. 20.—A FLOOD CHANNEL NEAR JERICHO, DRY EXCEPT FOR A FEW DAYS OR EVEN HOURS IN THE YEAR. (*Photo:* P. A. Buxton.)

Fig. 21.—BED OF A WADI AT BISKRA IN THE ALGERIAN SAHARA, SHOWING BUSHES OF OLEANDER (*Nerium*) AND TAMARISK (*Tamarix*). (*Photo:* V. H. W. Dowson.)

CHAPTER III

THE FLORAL ENVIRONMENT

I shall discuss the vegetation of deserts, not as a botanical problem, but because the plants are a very important element in the environment of the fauna. It will be appreciated that many of the characteristics of desert plants which are of great interest to the botanist, and to the study of which notable contributions have been made, appear to matter but little to the zoologist, who is interested not in the plants themselves, but in the plants considered as a part of the surroundings of the desert animals. It would be rash to say that such things as the pitted stomata and highly concentrated sap of plants growing in dry places do not affect the fauna, but at any rate it is not at present apparent that they do so. I have therefore omitted these and a number of other points to which the botanists have devoted attention.

It is impossible to draw up such a description of desert scenery and vegetation as would be applicable to the deserts of all the continents and both the hemispheres. It is, however, true to say that the prevailing tint for the greater part of the year is that of the soil, for the plants grow so far from one

another that they do not colour the landscape, except for a short period after rain has fallen. In most deserts bushes are rare and tend to become conspicuous features of the scenery, if they are present: trees are so rare that they are regarded with veneration by desert-dwelling races in more than one part of the world. At certain spots in the desert water is available in relatively large quantities: such spots are oases, and are characterized by a dense growth of vegetation, often consisting of plants which do not and cannot grow in the surrounding desert, and which are not found outside the oasis, until a second oasis is reached. This growth of vegetation provides food for a number of animals, many of which are specially dependent on one of the oasis plants, or for some other reason unable to live in the surrounding desert. The edge of an oasis is usually extremely sharply defined: the plants of the oasis grow up to the edge of the area which has the abundant water supply, and there they stop abruptly. Fig. 23 illustrates this admirably.[1] On the left is a dense growth of poplar, fig, apricot, bramble, and many other wild and cultivated plants, dependent on a perennial spring in the bottom of a "wadi": on the right, a yard or two away, is the "wilderness of Judæa," with no living plants except *Atriplex halimus*, and not many of that. The photograph was taken in July, after the spring annuals had died: their dried remains may still be seen. Fig. 22 gives a general view of the same country.

Very few natural oases exist, and many of them

[1] See also Fig. 10, opposite p. 42.

ig. 22.—Wilderness of Judæa, between Jerusalem and Jericho. (*Photo :* V. H. W. Dowson.)

Fig. 23.—Wadi Kelt, Wilderness of Judæa, Palestine. On the left are various Trees and Bushes; on the right is the barren wilderness. (*Photo :* P. A. Buxton.)

are only small thickets near such rivers as the Tigris and Zarafshan, which flow through deserts. Nearly all the larger natural oases have long ago been totally ruined by man, who has destroyed the characteristic and very local flora and fauna, planted carrots and cabbages and dates (Figs. 10, 12), and introduced along with them the common garden weeds and the common garden insect pests, so that to a naturalist a "well-developed" oasis is one of the most uninteresting sights in the world. The water which turns a given part of the desert into an oasis may come from any source, from springs, or seepage from a water-bearing stratum, from a passing river, or even from an artificial canal or artesian well.

The deserts of the Old World are great plains, and the vegetation is surprisingly monotonous and uniform over immense areas. Many genera and species of plants range from the western limits of the Sahara, or even from the barren parts of the Azores, Canary and Cape Verde Islands, eastwards to Sind and Turkestan. Conspicuous examples are the Colocynth (*Citrullus colocynthus*), the Saltbushes (*Suæda* and *Salsola*), and members of the genus *Zizyphus* (Fig. 25); very many others might be mentioned which are distributed over the greater part of the vast area. The uniformity of surface and of vegetation, which is so characteristic of the Old World deserts, is much less observable in America. MacDougal states that he found only thirteen species of flowering plants during a month's trip in the Libyan Desert: twelve of the thirteen belonged to very widely distributed species, and he

contrasts this with the fact that "many dozens of species are known from places in American deserts no larger than an ordinary farm, in single cañons, or on one slope of unique environic combinations." He suggests that the reason for this lies in the comparative newness of the American deserts, which consist of relatively small plains and steep mountains. The environment is varied and the plants vary with it. In the course of ages these deserts will undergo a process of base-levelling, and will perhaps come to resemble the immense desert plains of the Sahara, Mesopotamia, and Transcaspia. By that time the conditions will be so uniform, and have altered so profoundly from those now prevailing in America, that very many species will have ceased to exist. The relatively unspecialized types, which have not adapted themselves too closely to their environment, will have spread widely and come to occupy vast areas.

The plants which are found in deserts belong to special genera and species which are so modified in structure, and in their manner of performing their vital functions, that they can support life under very unfavourable conditions. These modifications are so great and so fundamental that the transfer of a desert plant to a less severe environment, or of a seaboard plant to the Arizona Desert, was always followed by the death of the plant, in certain of MacDougal's experiments; on the other hand, the transfer of plants to environments which were strange to them, but were not desert, resulted in quite a number of survivals.

We have already seen that the rigours of a desert climate abate in many places for a short season every year. Plant life in deserts has suited itself to the climatic conditions in many ways, of which three are the most important. During the short period which follows the rain annuals are common. At the same season a group of perennial plants which persist through the dry months dormant underground produces its leaves and flowers. The third principal group of desert plants consists of perennials the structure of whose aerial parts is so profoundly modified that they can continue their vital functions throughout the year. We shall now examine each of these groups more closely. The first group, the annuals, is extremely conspicuous after rain, so much so that for the moment the desert is no desert, and the perennials, at other seasons so conspicuous, cease to attract our notice. The seeds of the annuals have survived a dry period of months or years and have resisted terrific heat and desiccation, but the stems, leaves, and flowers are not anatomically modified for life in dry places. The annual plants appear shortly after a fall of rain, carpet the ground to a greater or lesser extent, blossom in an incredibly short time, and then wither rapidly when the soil and the air become dry. Figs. 24 and 25, taken in the plain of Jericho in February and June, show this. The spaniel dog illustrates the depth and thickness of the spring annuals. This ephemeral vegetation depends directly upon the rainfall, and on it in turn depend a large number of forms of animal life. In some parts of

the deserts of America there are two rainfalls: that which occurs in December and January is followed by crops of flowers of winter annuals: as soon as the cold weather is passed: these then dry up and perish. The summer rains come and soak the ground, but the seeds of the winter annuals do not germinate; instead, there comes up a crop of summer annuals which ripen seed soon after midsummer; this seed lies dormant all through the cold weather, even though it is saturated by the winter rains. Whether the desert has one rainy season or two these annual plants add very greatly to the number of species and of individual plants occurring in an area; in fact, a richness of flora is produced which for the moment far exceeds the inroads made upon it by the larger herbivorous animals: their number is limited by their ability to exist through the long dry seasons. The smaller forms of animal life, for instance, the insects, increase in numbers enormously as the annual vegetation grows, and like it rest in various ways for the rest of the year.

The second large biological group contains plants which exist beneath the ground during the dry months in a dormant condition, and which produce leaves, stems, and flowers after rain has fallen. The perennial part of the plant is a bulb, corm, tuber, or fleshy root. It is essentially an organ for storing food, and it is by drawing upon these reserves that the plant is able to respond rapidly to rainfall and send up its flowers and leaves: there is no occasion for the storage of water, for these plants are active only at a season when water is abundant. Plants

Figs. 24 and 25.—Photographs taken within a few hundred yards of one another in February (Fig. 24) and June (Fig. 25) at Jericho, Palestine. (*Photo:* P. A. Buxton.)

of this group are particularly common in the semi-deserts and deserts of Palestine, Sinai, Persia, and indeed in most parts of the Great Palæarctic Desert. Many of them belong to the Lily, Amaryllis, and Iris families, and familiar examples are colchicum, squills (the broad leaves of which are shown on the right in Fig. 26), tulips, asphodels, onions, and stars of Bethlehem. Their reserves of food are stored in different parts of the plant: in Stars of Bethlehem (Ornithogallum), onion (Allium), and others, in closely packed leaf-bases constituting a bulb; in iris, crocus, etc., in swollen subterranean stems (corms); and in the roots in asphodels and others.

The third important group in the flora contains those perennial forms which are so specialized that they can exist above ground and perform their vital functions at all seasons. To this end they are modified in many remarkable ways; roughly speaking, the modifications fall within two groups, those which tend to reduce the loss of water from the surface of the plant, and those which tend to preserve a store of water in the body of the plant. Many forms exhibit both types of modification. In the first group of adjustments to environment we find that the leaves are small or absent, or only produced after rain when the soil and the air are relatively damp; at such times loss of water from the surface of the leaf is of less importance than during the dry season. In those plants in which the leaves are greatly reduced or absent the twigs and stems are green; it is the chlorophyl in these organs which carries on the function of starch manufacture, a

function performed in ordinary plants by chlorophyl in the leaves. When leaves are present they are often extremely tough and leathery; the cuticle, in particular, is greatly thickened and the surface is protected in many species either with wax or with resins, or with incrusted salts, or with densely matted hairs: it is believed that all these modifications, which occur in desert plants of the most widely different families, enable the plant still further to reduce the amount of water which it loses by transpiration. In all deserts a certain proportion of the plants become succulent, that is to say, develop the capacity of storing a considerable quantity of water. Succulence is not only a characteristic of desert plants, but of those growing in any environment in which the available moisture is limited: some succulents, for instance, grow on salt-marshes, others on rock surfaces and roofs and walls, even in damp climates. Most of the desert succulents are found in areas with a rainfall which is slight but fairly regular, and they are not generally found in intense deserts and in climates without any regular precipitation. They are developed in an apparently capricious manner in certain deserts and not in others. For instance, the cacti, nearly all of which are succulent, some of them extremely so, are numerous both as species and as individuals in the deserts of the southern United States and of Mexico. In the arid parts of South Africa their place is taken by plants of the Spurge family (Euphorbiaceæ), and some of these plants so closely resemble the cacti of the New World that they can

Fig. 26.—The Mount of Temptation, near Jericho, Palestine, showing Spring Vegetation (February). (*Photo:* P. A. Buxton.)

Fig. 27.—*Calotropis procera* (Asclepiadaceæ), in the Plain of Jericho, Palestine. (*Photo:* P. A. Buxton. October, 1922.)

barely be distinguished from them until they flower. This is an example of convergence, the production of very similar structures by plants which are not at all related to one another, as a response to similar environmental influences. On the other hand, succulents are rare in the Great Palæarctic Desert, speaking generally, and the cause is unknown, for in many places the conditions of weather and soil are such as appear to favour succulents in American and other deserts. The only noteworthy exception is the salt parts of the Great Palæarctic Desert: in these such genera occur as are familiar in saltings in many parts of the world.

Nearly every part of the plant body, but most commonly stems and leaves, may be used for the storage of water. In the Cactus family, for instance, the stem is greatly thickened and often nearly globular: it is used for the storage of water, and MacDougal states that tree cactuses may contain as much as a thousand gallons. Succulence of the stem occurs also in spurges and many other families: in Southern Mexico there is an Ipomæa, a plant closely allied to the convolvulus, which has a soft thick trunk containing water, and Beaucarnea, a relative of the Yuccas, is so charged with water that its trunk is 7 or 8 feet in diameter, though the tree itself is not above 25 feet high. An example of a plant with succulent leaves, *Calotropis procera* (Asclepiadaceæ) is shown in Fig. 27.

It will be seen that there is a most interesting contrast between the second and third groups of desert plants. Members of the second group have

little need for a reserve of water, for they are only active after rain when the soil is damp; they store food in the form of starch and allied substances, so that when the rain is received they can at once produce active growth. Members of the third group are active at all seasons; they therefore are able to manufacture their own food as they need it: many of them possess storage organs, but they store water not food.

The sap of many succulent plants is saline or bitter: this appears to protect the plant from animals in many instances, but it does not follow that the primary function of the bitterness is protective. In certain instances it is known that the water accumulated by succulent plants is of use to animals; for instance, the donkey can be watered with the juice of the giant cactus (*Cereus giganteus*), which is too bitter for man's use, and the barrel cactus (Echinocactus) furnishes several pints of fluid which even man drinks readily.

Thorniness is possibly more characteristic of the third group of desert plants than succulence: it is a character common to the plants of deserts in all countries, and of every type of desert, and it is exhibited by herbs and bushes belonging to a very great number of different natural orders. It is found on the most varied parts of the plant body; the stem may be thorny, and the leaves may be covered with thorns, or may themselves be transformed into thorns; the fruits also may be thorny. It is believed by many that the thorns protect the plant against herbivorous animals. This point will

be considered in greater detail in the chapter which considers the relationships between plants and animals in the desert. Here I shall only say that the view that thorns are defensive is difficult to maintain, except in a few special instances. On the contrary, it appears probable that the thorniness of the plants that grow in deserts is due rather to physical than biological influences. It is known that if a plant is grown in a dry atmosphere it produces a relative increase of various hard substances at the expense of its starches and plastic materials; it is also known that cultivation in a damp atmosphere retards the development of thorns in seedlings. It is therefore possible that the thorniness of desert plants is a purely physical or chemical phenomenon, and that any protection that the plant derives from it is purely incidental.

CHAPTER IV

ANIMALS AND THE PHYSICAL ENVIRONMENT: GENERAL RELATIONSHIPS

General Relationships

We have considered the surroundings in which the desert animals live, and seen that the climate and other physical factors are generally unfavourable to ordinary animal life. We shall now study some of the adaptations which enable the animals to overcome the obstacles of their physical environment, and to draw sustenance from the specialized flora of the desert.

Every element of the desert climate is liable to rapid fluctuations, which are often quite irregular: and in many desert places the great heat and drought, and violent winds and other climatic factors, all combine during the summer to be most hostile to the flora and fauna.

The habit of æstivation in plants has been already referred to (pages 57–59). A similar habit is common in the invertebrate animals of desert faunas. In the present state of knowledge we can only attribute it in broad terms to the extreme hostility of the summer climate; but it may well be that as we study the effects of varying temperature, or humidity,

or other conditions, upon particular species, our knowledge will become more accurate. We shall perhaps find that in the case of one creature the cessation of activity during summer is induced by a mean temperature above a certain degree, or in another by a minimum daily humidity below a certain percentage. Until the particular effect of altered climatic conditions upon selected species of animals has been studied we cannot do more than record the facts, which are that the great majority of the invertebrata in deserts undergo periods of dormancy either in winter or in summer, or both.

In Mesopotamia it is easy to notice that insects are commonest after the winter rains, during the temperate spring and early summer. From April to June nearly all insect life is fully active, and its activity coincides with and follows the rapid growth and blossoming of the spring vegetation. During the hot dry months of summer the insects are not in evidence; as the weather becomes cooler there is a distinct, though less evident, increase in the number of insects on the wing. Figs. 28 to 30 are compiled from collections made at Amara, R. Tigris, by Capt. W. E. Evans, R.A.M.C., and myself. It would scarcely be extravagant to claim that our collections are a fair random sample of the fauna of Amara at all seasons. We had few distractions and were deeply interested in entomology; we each resided in Amara for almost exactly one year; we felt that we were in an unknown land and therefore collected everything, even species which were common, in long series when we could; we could

identify none of our captures and therefore did not discriminate; and we generally worked independently, in different parts of the area round Amara. Fig. 28 shows the monthly occurrence and relative frequency of certain families of Orthoptera. It will be seen that the Praying Mantis family was represented by most species in April and September;

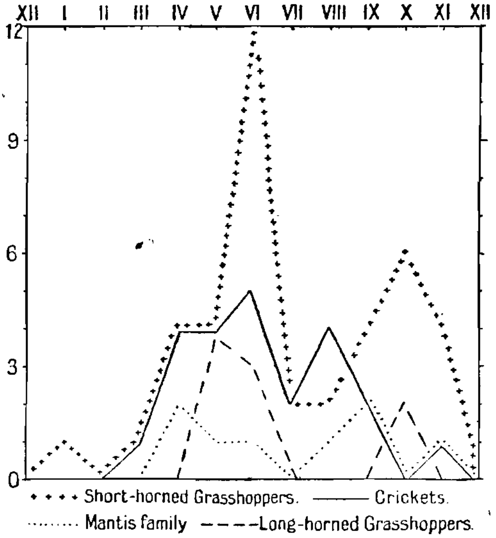


Fig. 28.—Number of Species of Certain Families of Orthoptera present month by month in Collections made at Amara, Lower Mesopotamia, by W. E. Evans and the Author. The Months are shown by Roman Figures, the Number of Species occurring by Arabic Figures.

the Long-horned Grasshopper family in May and October; and that of the Short-horned Grasshoppers in June and October. The Crickets, which are nocturnal and shelter by day under logs and in holes and cracks in the ground, do not show this seasonal incidence; the conditions to which they are exposed are different and they react differently to them. The Hymenoptera (Fig. 29) show similar

curves; the Fossors are most abundant in June and September; the bees in July and September. The Ruby Wasps (Chrysids) and Wasps (Vespids) were represented by so few species that curves have not been constructed from them, but the curve for all four families shows maxima in June and September. Even the moths comply in the main with this rule, which could hardly be expected, as the majority of them are nocturnal, and shelter

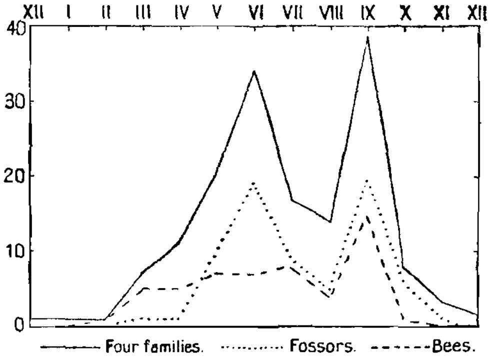


Fig. 29.—Graph similar to Fig. 28, showing the Monthly Prevalence of the Fossors ("Solitary Wasps"), Bees, and "Four Families" of Hymenoptera (i.e. Fossors, True Wasps, Bees, and Ruby Wasps) at Amara.

by day in places in which they must be protected from the great heat and low humidity. The curves in Fig. 30 all reach maxima in May or June, and in September.

Certain groups of insects showed a different seasonal prevalence, amongst others some of the butterflies, of which very few species were found at Amara. The Clouded Yellow (*Colias croceus* = *edusa*), Common White (*Pieris rapæ*), and three Blues (*Zizera karsandra, Tarucus balcanica,* and *T. mediter-*

raneæ) were all on the wing from March to June and again from September to November. A few individuals of several of these species were taken in the intervening hot months, but these species were rare at that season and clearly fall into the same group as the Orthoptera, Moths, and Hymenoptera (Figs. 28 to 30). Three species, however, had totally different seasons. One "Blue" (*Chilades galba*)

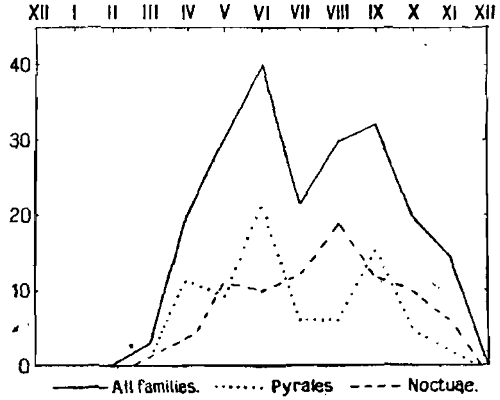


Fig. 30.—Graph similar to Fig. 28, showing the Monthly Prevalence of Pyrale and of Noctuid Moths and of all Families of Moths except Pterophorina, Tortricina, and Tincina.

was abundant from June to August and was not taken at other seasons, though its food plant was always abundant and was in leaf all the summer and autumn; the "Skipper" *Parnara matthias* was only taken from June to November; and the common salmon-coloured *Teracolus fausta* from July to December.

The apparent absence of this species in spring and early summer may be due to one of two causes. The Caper bush (*Capparis spinosa*), its food plant,

is bare of leaves till the warm weather is well advanced, and it is possible that the species lies dormant through the spring as egg, or resting larva, or pupa, until the Caper bush is in full leaf. On the other hand, it is possible that even the mild winter of Mesopotamia is fatal to *T. fausta* in all stages, and that it recolonizes this country every spring by immigration from lands with warmer winters; in Palestine it seems extremely probable that this species dies out every winter, and recolonizes the land every spring.

It is convenient to mention here another Pierine butterfly which eats Caper, the species known as *Belenois mesentina*, although it was apparently absent from Amara. It is a species which often occurs in great numbers in very hot places, even in the hottest weather: for instance, along the North-West Frontier of India it is common from May to October, a season during which the other butterflies are scarce or not on the wing at all. It has an extremely wide distribution, from tropical Africa to India, and is by no means confined to deserts. This wide distribution is possibly due to its ability to continue active life at a time of year when heat and dryness have caused most butterflies to cease from flying, and this activity in the height of summer may in turn be due to the fact that the Caper is one of the not very numerous plants in full leaf at that season.

It must be admitted that this study of the number of species of insects on the wing in various months is liable to one very grave criticism. Each group

of insects, in fact each species, finds this or that month favourable to it for a different reason. The mantises may be influenced by an abundance of other insects on which they prey. The bees or wasps may, for all we know to the contrary, time their emergence more by the flowering season of certain plants than directly by any climatological event. The moths may fly at midsummer, not because midsummer conditions suit them particularly, but because several months before there was abundance of herbage for their larvæ. In fact, Figs. 28 to 30 represent facts which are the result of the action of very many factors: they cannot be used as a basis of a theory. If we wish to interpret the abundance of insects in a certain month, we must take individual species of insects and study their reactions to altered temperature, humidity, food, soil, moisture, etc. We are not justified in taking such curves as Figs. 28 to 30 and comparing them without further analysis with the meteorological statistics, or the season of greatest plant growth.

In the British Isles we are accustomed to think that the warmer the temperature to which insects are exposed, the more quickly do they go through the various stages of their life-history. This is clearly a fallacy, because in Mesopotamia in many different families of insects active life is in abeyance during the hottest months. We can at present only guess at the cause; it is probable that heat and humidity interact in such a way that neither factor can be considered separately: a certain high

temperature is optimum for the development of a certain insect only when the humidity is about a certain figure; if the humidity is much below that figure the temperature may be unfavourable or even fatal.

The curves in Figs. 28 to 30 show clearly that the cessation of active life in summer is less than that in winter. One is accustomed to associate the summer of Mesopotamia with fierce heat, acute discomfort and the sudden death of Europeans who were unable to avoid active work in the middle of the day: apparently to the adult insect the summer is less unfavourable than the winter, for it will be seen that January provides far fewer winged insects than July or August. Our conclusion, then, is this: that æstivation and hibernation are common phenomena among desert insects; until we have accumulated a mass of detailed analysis we must accept it that these phenomena are, in a general way, due to the climate in summer and winter being unfavourable.

Ants, as Wheeler has shown, adapt themselves to the desert seasons in several ways. In more ordinary surroundings some ants are insect-eaters, but very many live upon plant juices which they obtain either directly or from Plant-lice (Aphidæ) and Scale insects (Coccidæ): in deserts they have to contend against periods of drought. Some of them therefore become extremely active predators, ranging far and wide and running with great rapidity. Many others collect seeds and pieces of dried plants, and depend upon this harvest for food and moisture during the summer. Others, again, collect plant juices, and

the secretions of Plant-lice during the season of active growth which follows rain, and store these fluids in the stomachs of certain specialized "worker" ants; these become enormously distended with fluids, and are known as honey-pot ants, and from them moisture is obtained during the dry period. There are several genera (*Camponotus*, *Myrmecocystus*, *Melophorus*) in which this habit has been developed, and they are found both in the American and Australian deserts.

It is natural that, just as the insects are most numerous in the clement spring and temperate autumn, so they are much more numerous in a season following good spring rains and a normal flood than in a year in which moisture and therefore annual flowers have been deficient. In this connection the enormous variations from the normal which characterize the annual rainfall of deserts (pages 11–13) will be remembered. If the regular winter rains are deficient the annual plants and the butterflies, bees, and other insects are scarce as regards individuals; apparently also certain species are entirely absent, at any rate they are so rare that they are not detected. The possibility that insects and plants can "carry over" an unfavourable period not of months but of years requires investigation, but there is a good deal of evidence to suggest that it may indeed be so. For instance, Hartert was in the country south of Biskra, Algerian Sahara, in 1908 and 1909: he noticed white butterflies very rarely between Biskra and Borj Saada, and none between Borj Saada and Tuggurt. In 1912, after

good winter rains, he travelled along the same road, at the same season. He saw dozens of white butterflies between Biskra and Borj Saada, and hundreds of Melitæa and Euchlöe between that place and Tuggurt.

Spencer's observations upon the small mammals and other creatures of Central Australia, and the effect upon them of "good" and "bad" years, are extremely interesting. After the wet season the reproduction of the small rodents and marsupials is at its height; the succeeding drought kills a very large number of them, especially the immature individuals, and the few survivors attain maturity without attaining the dimensions of individuals reared under more favourable conditions; for instance, the adult males of the marsupial *Phascogale cristicauda* may vary in length from 136 to 220 millimetres, and females carrying young from 125 to 170 millimetres. A succession of dry years not only greatly reduces the numbers of small mammals, but also reduces their powers of reproduction. Thus the small, mouse-like marsupial *Sminthopsis crassicaudata*, which has typically ten nipples, produces ten young at a birth in seasons of plenty, and not more than four or five in seasons of scarcity. "If the drought be abnormally prolonged then even the hardiest animals will suffer, and the fauna will be so reduced that it may take some time before increased fertility on the part of the survivors and the influx of immigrants from the broad belt of land enclosing the central region will make good the deficiency" (Spencer).

The effects of good rain upon bird life is illustrated by Ticehurst's observation that the White-cheeked Bulbul (*Pycnonotus l. leucotis*) of Sind, which normally breeds in March and April, breeds again in September in years in which much rain has fallen. The fact that this bird is a denizen rather of thickets and gardens than of the bare desert does not render it unsuitable for inclusion in our study of the biology of deserts, for the conditions of climate and the variations between "good" and "bad" years are essentially the same in the desert as in the oasis. It seems that this observation and Spencer's upon the small marsupials are best included here rather than in the section which deals expressly with water, because quite clearly the increased reproduction of bird or marsupial is not to be ascribed directly to the rainfall but to some much more general effect of the rainfall upon vegetation, insects, etc., and so indirectly upon the larger creatures.

The present is a convenient place for considering a remarkable type of small mammal which has been evolved repeatedly in deserts and semi-deserts, and not in any other environment: as we are ignorant of the causes which have contributed to the production of this type it appears best to group it with other general relationships with the physical environment. The mammalian type to which I refer is most familiar to us in the Jerboa (Fig. 31). This is a rodent about the size of a rat, provided with short fore-limbs, which are not remarkable, and excessively long hind-legs and long, narrow feet; the toes are reduced in number to two; the tail

is very long, covered with short hairs, and bearing at its tip a large tuft. The short fore-limbs are used for burrowing, holding food, and apparently also for lifting water to the mouth (page 90): the length of the hind-limbs is correlated with the habit of progressing by leaping and not by running, and it is possible that they serve also to give the Jerboa and the animals which resemble it an in-

Fig. 31. Hairy-footed Jerboa (*Jaculus jaculus*) from Egypt.
Notice the long hind-legs with reduced number of toes, and the long tail with a terminal tuft of hair, and the biped attitude. (*Drawn from life by* Miss A. M. Gayton.)

creased power of observing the approach of enemies on the bare ground. The speed which a Jerboa can attain by jumping, and the great irregularity of its movements, undoubtedly make it extremely difficult to capture, a fact which can be verified if you liberate a Jerboa in the confined space of a room and endeavour to catch it in a butterfly net. The Jerboas (Dipus and Jaculus) belong to the Dipodidæ, a family of Rodentia of which all the

members are modified in the same direction as the Jerboa, though not all to the same extent. In Allactaga, for instance, five toes are present on the hind-foot, though two are vestigial; in Scarturus the first digit is absent, and the fifth vestigial; in Dipus and Jaculus only three toes are present, and the two which are lacking are not represented by any vestige externally (Fig. 32).

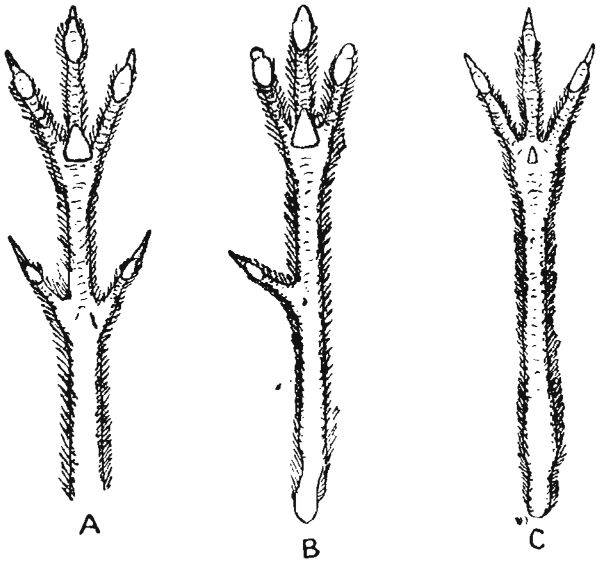


Fig. 32.—Under-surface of Right Foot of *Allactaga indica* (*A*), *Scarturus tetradactyla* (*B*), and *Jaculus jaculus* (*C*).
(*After* R. I. Pocock.)

These genera are characteristic of the Great Palæarctic Desert and of the steppes on its fringe; the closely related Zapus is American, and is interesting because it is intermediate in habit and anatomy between the ordinary running quadruped mice and the biped jumping Jerboas. In another

family of rodents, the Muridæ, the same modification of form may be seen in desert species belonging to two of the sub-families. Of the first, the Gerbillinæ, or Gerbils [1] (Fig. 33), no member has become completely biped, but nearly all the genera and species show some lengthening of the hind-leg and hind-foot and tend to progress at times by running, at others by leaping. The species figured

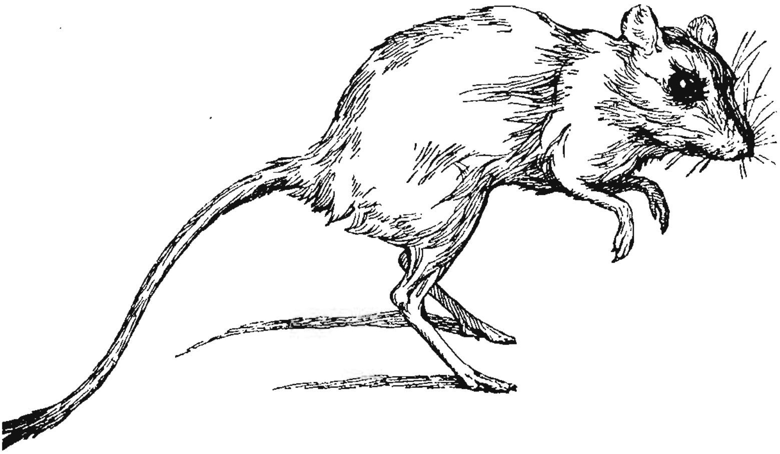


Fig. 33.—East African Gerbil (*Taterona vicina*) from East Africa. This animal is typical of a very large number of species, most of which are found in various parts of the Great Palæarctic Desert. (*Drawn from life by* Miss A. M. Gayton.)

(*Taterona vicina*) shows these characteristics well, and is drawn from life in a characteristic biped attitude. Other Gerbils (e.g. Meriones) are more rat-like in form and in habit. In the second sub-family, the Murinæ or True Mice, occur Conilurus and Notomys in the Australian deserts, exhibiting various stages in the lengthening of legs and feet

[1] Examples are Meriones (pages 92, 130, etc.), Gerbillus (page 138), and Dipodillus (pages 103, 127).

and the assumption of the biped habit. In the deserts of the southern part of North America animals resembling Jerboas have been evolved from yet another family of rodents, the Heteromyidæ.

The rodents which have already been mentioned all belong to the section Myomorpha; in another section, the Hystricomorpha, and not closely related to the forms which have been considered, is the Cape Jumping Hare (Pedetes). This animal is much larger than any Jerboa, but resembles that animal in its long hind-legs and long tail: it feeds on all fours, but when it is pursued it escapes by prodigious leaps. It lives in arid and desert places in Africa from Mozambique southwards.

It is surprising to find similar "Jerboa-like" animals among the totally unrelated marsupials: good examples are *Phascogale Hillieri* and Antechinomys. The last lives in Central Australia in sandy plains among tussocks of grass in the same environment as the rodents Conilurus and *Mus gouldi*. The Antechinomys and Conilurus are Jerboa-like, progress by jumping, and show remarkable general similarity in form; the Mus, which is equally common, and apparently quite as successful in the business of life, is an ordinary mouse, and progresses by running: it is difficult to see why the jumping habit has been evolved in the Conilurus and Antechinomys unless, as Spencer suggests, the resultant irregularity in movement tends to baffle small hawks chasing them. Conilurus is an extremely abundant rodent; Antechinomys, which

so closely resembles it in habits and shape, is very rare, possibly because it is an insect-eater (page 83). Every one of these small Jerboa-like creatures exhibits the coloration typical of so many desert animals (page 141), the sandy, unicolorous upper surface, and white belly.

For the following tables I am indebted to the kindness of Mr. O. Thomas, F.R.S., of the British Museum (Natural History). The first makes clear the relationships of the forms of which I have been speaking; it shows that animals outwardly resembling the Jerboa have been evolved on a number of different occasions, apparently as a response to the conditions of life in a desert, and that in each continent the Jerboa-like animal has been produced from a different family or sub-family.

Order.	Section.	Family.	Sub-family.	Genus.	Habitat.
Rodentia .	Myomorpha	Dipodidæ	Dipodinæ	Allactaga Dipus Jaculus	Great Palæarctic Desert
,, .	,,	,,	Zapodinæ	Zapus	America
,,	,,	Muridæ	Murinæ	Conilurus Notomys	Australia ,,
,, .	,,	,,	Gerbillinæ	Gerbillus Meriones Dipodillus	Great Palæarctic Desert
.	,,	Heteromyidæ		Dipodomys Perognathus	America ,,
,, .	Hystricomorpha	Pedetidæ		Pedetes	S. Africa
Marsupialia .	Polyprotodontia	Dasyuridæ	Dasyurinæ	Antechinomys Phascogale	Australia ,,

The second table shows at a glance the number of toes present in these Jerboa-like animals, and emphasizes the fact that a reduction in the number of toes has repeatedly taken place. Five is of

course the full number of digits in either the fore- or the hind-foot. "4 and 1" or "3 and 2" indicate that 4 (or 3) normal digits are present and 1 (or 2) which is reduced in size. Toes are only shown as "vestigial" when they are minute, and probably not used: thus Perognathus has five digits on the hand, of which one is small: on the foot it has either three normal toes and two small ones, or else (in another species) three normal toes, one small and one vestigial. A zero in the "vestigial" column indicates that no external trace of digit can be found. In Dipus and Jaculus the reduction has gone so far that two toes are not even represented by a vestige.

Genus.	Number of Toes.		
	Fore-foot.	Hind-foot.	
		Functional.	Vestigial.
Dipus, Jaculus	4 & 1	3	0
Scarturus	4 & 1	3	1
Allactaga	4 & 1	3	2
Gerbillus	4 & 1	3 & 2	
Zapus	4 & 1	3 & 2	
Perognathus, either	4 & 1	3 & 2	
or	4 & 1	3 & 1	1
Conilurus	4 & 1	3 & 2	
Notomys	4 & 1	3 & 1	1
Antechinomys	4 & 1	4	0
Phascogale hillieri	5	4	1
Pedetes	5	4	0

CHAPTER V

ANIMALS AND THE PHYSICAL ENVIRONMENT (*continued*)

i. Water Supplies. ii. Fauna of Waters in Deserts. iii. Heat and Relative Humidity. iv. Animals and Wind. v. Relationships with Soil.

i. Water Supplies

I propose to marshal some of the available facts which relate to the reaction of the desert animals to drought, heat, wind, and other particular elements in the climate, and to deal first with the means adopted by the animals for making the most of a scanty and irregular water supply. In many semi-deserts and in all deserts rain falls at such rare intervals that life would be impossible to any species directly and solely dependent on it, but other sources of water are available, and probably on the whole more important. Perhaps the most obvious is the dew. Meteorological records of dew-fall are scanty from all parts of the world, and observation of dew-drinking by small animals are very few. Atkinson, writing of his experiences at Abu Kir in Egypt, remarks: "The water supply of the numerous beetles inhabiting the patches of baked clay in the coastal deserts

was a puzzle to the writer till it was noticed that they drank drops of dew from the angles of dried-up thorny plants."

Though lack of precise observation prevents us from forming a clear idea of the importance of dew to the fauna, it is probably considerable, at any rate at certain seasons. A more constant source of supply is the desert vegetation. Plants, however dead they are, and however long they have been exposed to the desert wind and sun, are not chemically dry, any more than hay or chaff are dry. It has also been suggested that during digestion by an animal a certain additional amount of water may be elaborated as a by-product of the break-down of the complex chemical bodies of which the plant consists.

One can therefore understand that it is possible for a seed-eating mammal or bird to exist for long periods without eating succulent plants or drinking the dew or obtaining water from any visible source, and some of them can do this. I remember an Egyptian Jerboa which was kept by a member of my family as a pet. It was given no water and lived for many months on crushed oats and bran; when it was offered apple or carrot or other moist food it generally refused to eat it. That it could not drink dew is certain because it lived in a London house. It is almost certain that many birds, insects, and small mammals depend solely upon the minute quantities of water to be found in seeds and dead plants which have become completely "air-dry."

It is reasonable to suppose that just as some animals obtain their small requirements of water from the plants they eat, so others obtain their supply from the ants, grasshoppers, etc., which are their staple food: such cases are probably few because animals which are dependent upon insects for their food and drink are uncommon in all deserts: this applies not only to the order Insectivora but also to insect-eating members of other orders. This rarity is due in all probability to the great seasonal fluctuation which occurs in the number of insects, and that in turn follows the enormous variations in climate to which all deserts are subject. In the Great Palæarctic Desert I know of no purely insectivorous [1] mammal, except the bats. Of the food of such resident birds as the Desert Warbler (*Sylvia nana*), which is probably a pure insectivora, we have no accurate information. In the Australian deserts the ants are a dominant group: it appears that they are the staple food of *Myrmecobius*, a marsupial ant-eater, which devours them above ground, and of *Notoryctes*, the marsupial mole, which lives beneath the surface.

Actual water-holes, springs, rivers, etc., provide water to the creatures which live on their banks, and to a number of others which come in from the surrounding deserts to drink. Among them are many birds, and bats, a few insects, and many large terrestrial mammals.

[1] The hedgehogs which inhabit many parts of this area (e.g. *Hemiechinus auritus*), though "Insectivora" in the technical sense, are not an exception to this statement, for they are by no means exclusively eaters of insects.

Among birds which fly to water the most remarkable are the Sandgrouse (Fig. 34). Sportsmen are aware that the various species of Sandgrouse (Pterocles and other genera) which inhabit nearly every part of the Great Palæarctic Desert water at certain spots on the banks of rivers, at certain regular hours. There is good evidence that the birds fly in from very many miles, and as the chosen watering-place is often very circumscribed, immense numbers of birds congregate there for a very short period every day. Different species of Sandgrouse water at different times of day, the majority in the early morning, Lichtenstein's Sandgrouse before sunrise, or even in the middle of the night when there is moonlight. Sandgrouse normally stand in shallow water when drinking, and as their legs are short their breasts become saturated with water. This is true of both sexes and happens at all seasons. It is reasonable to suppose that from this has developed their very remarkable manner of supplying water to their chicks. Native hunters have always asserted that they carry water to their young in the hot, bare desert in their saturated breast plumage. That this is correct has been proved by Meade-Waldo, who has had many broods of Sandgrouse (fifty-one of *Pterocles alcatus,* seven of *P. exustus,* and three of *P. arenarius*) hatched in his aviaries. The young feed themselves on small seeds from the time of their emergence from the egg, and are attended by both parents. "The male rubs his breast violently up and down on the ground—a motion quite distinct from dusting,—and

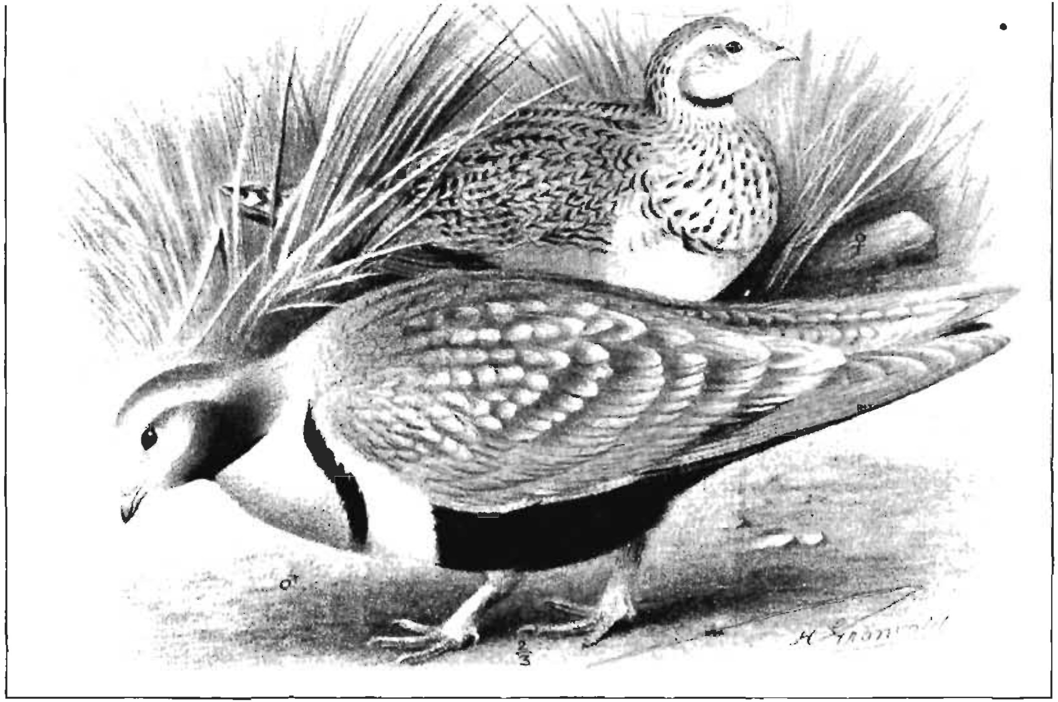


Fig. 34.—Imperial Sandgrouse (*Pterocles arenarius*). (*After* E. C. Stuart Baker.)

when his feathers are awry gets into his drinking-water and saturates the feathers of his underparts. When soaked he goes through the motion of flying away, nodding his head, etc.; then, rememberng his family is close by, he would run to the hen, make a demonstration, when the young run out, get under him, and suck the water from his breast —the appearance being that of a mammal suckling her young. The young pass the feathers through their bills, and keep changing places until the supply becomes exhausted. Until the young can fly *they take water in no other way*, and the cock gives it to the young *only*." (Meade-Waldo.) As soon as the chicks can fly they cease entirely to drink from the males' breast-feathers. Sandgrouse in nature breed at various dates, but one may say roughly that they choose the hot weather. The following are dates on which eggs of certain species have been found in various places:

Western Pintailed Sandgrouse	May	Spain.
Eastern Pintailed Sandgrouse	May, June, July	Mesopotamia.
Spotted Sandgrouse	April, May, June, July	Mesopotamia.
Little Pintailed Sandgrouse	Throughout the year, especially March to July	Punjab.
Pallas' Sandgrouse	March to June	Central Asia.

It seems that many young Sandgrouse are brought

into the world when the air is hot and dry, when the desert soil is so hot that you cannot keep your hand on it, and when the vegetation is parched and the seeds on which they feed are already air-dry. They run about, even during the hot hours, near their parents but not sheltered by them, as I have myself seen at Mandali on the Perso-Mesopotamian frontier in August. As their only means of maintaining a body temperature of about 100° F. while they run in a dry atmosphere on desert, the surface of which is 150° F. or higher, is by evaporating water, it is not remarkable that special methods have been evolved to bring water to them in their waterless home. What is remarkable is that the other desert birds appear to live successfully without watering their chicks at all. The Crested Larks (*Galerida cristata* and *G. theklæ*) fly regularly to water in the evening when water is available near their haunts, though there is no evidence that this habit is invariable or obligatory; the Stone Curlew (*Œdicnemus*) and Coursers (*Cursorius*) do the same, at any rate sometimes.

Ticehurst, writing of the birds of Sind, states that the Trumpeter Bullfinch (*Erythrospiza githagineus crassirostris*) drinks nearly every hour, and that the Striated Bunting (*Emberiza s. striolata*) drinks at frequent intervals during the day. So far as we know none of the small desert birds give water to their young by regurgitation, and certainly none carry water in their breast-feathers. There is a group of birds which seem to be entirely independent of water, or rather to depend solely on

the water which they can obtain from dew, insects, and the vegetation ; in this group fall the Houbara Bustard (*Chlamydotis undulata*), the Chough Thrushes (Podoces), the Larks Alæmon and Ammomanes, and others.

Certain birds inhabit the fringe of deserts, but seem to be prevented from penetrating them because they cannot dispense with drinking. The need for a drink of water is in these cases a limiting factor in their distribution. An excellent example is the Black Partridge (*Francolinus vulgaris*), an abundant bird in the Mesopotamian plain. It is never found more than a couple of hundred yards from water; it is a lover of thick scrub, but where scrub occurs far from water the Black Partridge cannot be found. In California a somewhat similar case occurs. The Desert Quail (*Lophortyx gambeli*) wanders out into the desert to forage, but its real home is in the scrub along the banks of the California River: it requires to drink every morning and evening.

It is difficult to study the habits of bats. Certainly many desert-dwelling species visit water regularly at the beginning of their evening flight, but we have no reason to say that this is the custom of desert bats in general.

Many wasps and other Hymenoptera make long flights to drink, and crowd any spot at which they can obtain water : some species require also mud for nest-building. In Mesopotamia one often observed the Oriental Hornet (*Vespa orientalis*) drinking greedily in mess-rooms, and drowning itself in drinking-cups : this had a considerable hygienic

importance, for the hornet was a filthy feeder and was frequently loaded with bacteria derived from the human intestine.

Among the large mammalia there are many species which drink, and drink freely, when an opportunity is given them, but which are able to dispense with drinking when it is necessary. They derive a considerable quantity of water from the vegetation which they eat, and one need hardly say that the amount of vegetation, and of moisture in it, varies very greatly with the season. Thus Doughty observed in Arabia that "the camels now feeding in the sappy rabbia (spring pasturage) were jezzin or 'not drinking.' In good spring years they are in these diras almost two and a half months jezzin, and are not driven to the watering." Gregory quotes very similar facts from Australia: he says that in 1891 Tietkin marched 537 miles in thirty-four days without watering his camels, and that Phillipson kept a herd without water in a sand-hill country for two months. On the other hand, if very little grazing, or none at all, can be obtained and if camels are doing hard work, their endurance is very much less. Augièras speaks of sixteen days' march without water in the Central Sahara as a severe trial to his camels, and Haywood gives one to understand that about eight days is near the camel's limit in midsummer in Tanezruft, a district of the Sahara which at that season is entirely devoid of any grazing. Camels not only possess this remarkable power of abstaining from drinking for long periods, but they are able to drink salt and bitter water which man

and horses cannot swallow; when water is available their consumption is low, about seven gallons daily compared with the horse's thirty. Other large creatures which are able to dispense with drinking, but which drink when they have opportunity, are the ostrich, the giraffe, the eland, and probably many other antelopes from the parts of tropical Africa which are rather semi-arid grass-land than desert.

In desert of an extreme type many of the animals have perforce to dispense entirely with drinking water, and it appears that a certain number of species never drink at all, and derive their whole water-supply from the desert herbage, and possibly the dew. In this category of total abstainers Abel Chapman mentions the Addax (Fig. 35) and Oryx (Fig. 36) antelopes and the Addra and Sudan gazelles, all of them inhabitants of the Anglo-Egyptian Sudan. He also states that on certain small islands in the Red Sea *Gazella arabica* exists as a dwarf race, not exceeding one-third of the weight of the normal race, and that these islands are entirely without water.

It is probable that this ability to dispense with water is a character of many of the gazelles (Fig. 37), and that it accounts for the fact that species of the genus are found almost throughout the Great Palæarctic Desert.

Grinnell and Dixon state that the Round-tailed Ground Squirrel (*Citellus tereticaudus*) does not drink even when it has the opportunity; another species, the Desert Antelope Ground Squirrel (*Ammospermo-*

philus leucurus), can last for several months between drinks, but does drink, in nature, when water is available. We know almost nothing of the water needs of our Old World rodents. I have already recounted observations made on a captive Egyptian

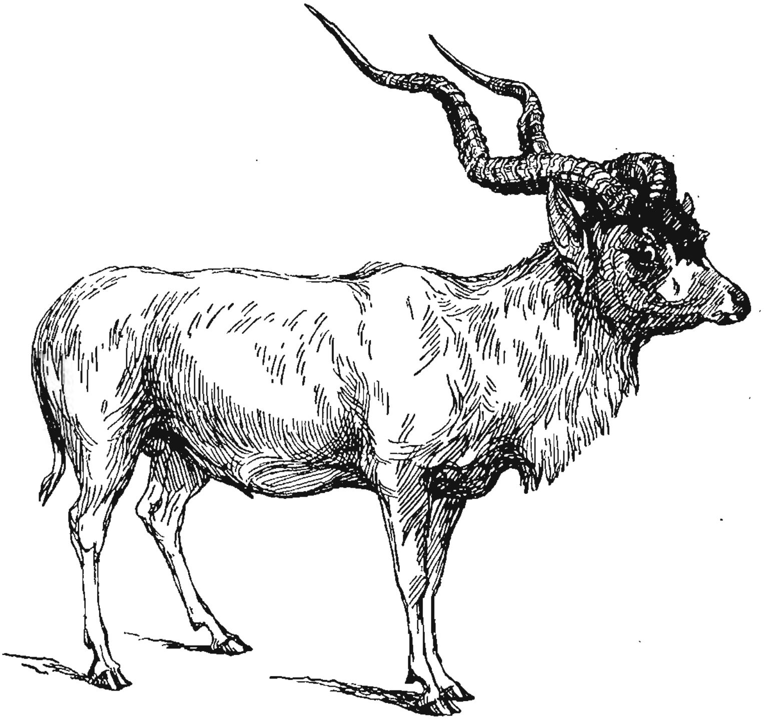


FIG. 35.—ADDAX ANTELOPE (*Addax nasomaculatus*), MALE, FROM THE SUDAN.

(*Drawn from life by* Miss A. M. Gayton.)

Jerboa in London: Cheeseman kept captive specimens of a different species (*Jaculus loftusi*) in Basra, Mesopotamia, in summer, and remarked that "they drank frequently, taking small sips in their forepaws. This is remarkable, as their earths are often placed

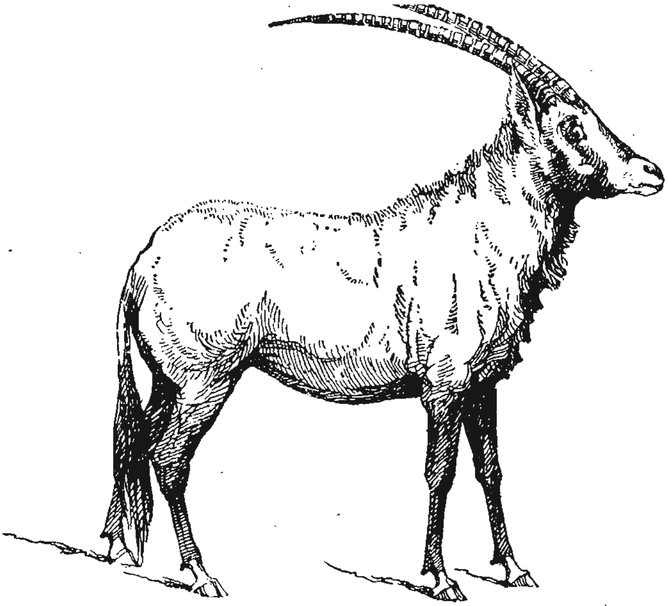


Fig. 36.—Arabian Oryx (*Oryx leucoryx*), an Inhabitant of Waterless Sandy Desert.

(*Drawn from life by* Miss A. M. Gayton.)

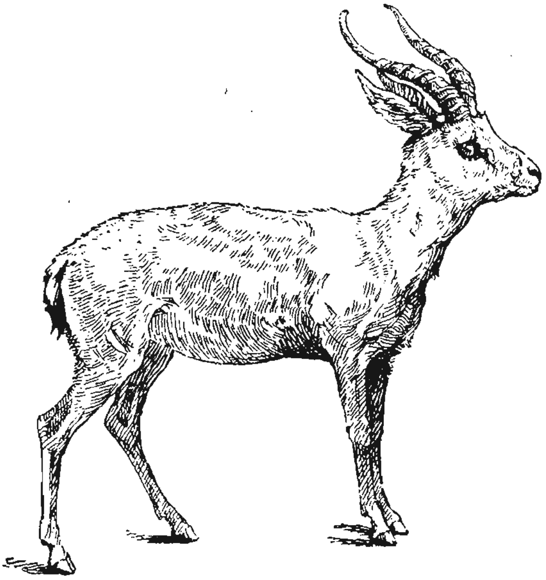


Fig. 37.—Persian Gazelle (*Gazella subgutturosa*), from **Kirkuk, Perso-**Mesopotamian Frontier.

(*Drawn from life by* Miss A. M. Gayton.)

where both dew and water would be to all appearances unobtainable." Probably, therefore, this Jerboa is to be grouped with the animals which do drink, but need not do so. The Gerbil *Meriones swinhoeii*, from the flat stony uplands of the Afghan Border, refuses water in captivity (C. M. Ingoldby).

According to Camp, most American desert reptiles require no water, and this must be true of many which occur in the Great Palæarctic Desert: my correspondent, Capt. G. W. G. Hingston, supplies a good example in the Agama, which frequents the ruins of Ur of the Chaldees in Southern Mesopotamia, a dusty spot far from the River Euphrates or any well, and without rain or vegetation for at least seven months in the year. The lizard *Moloch horridus* of West and South Australia, a repulsive animal covered with tubercles and spines, has the power of absorbing water through the skin after a fall of rain. The Gecko (*Eublepharis macularis*), which occurs in Persia and North-west India, drinks freely from a saucer in captivity (C. M. Ingoldby).

As our knowledge of the biology of the smaller forms of desert life increases we shall no doubt find remarkable instances of ability to exist without moisture. The case of a Stratiomyid fly (*Hermetia chrysophila*), the larvæ of which are able to endure at least fifteen months without food or water, and which eat decayed cactus joints whenever moisture is present, is probably typical of a large number of other insects.

ii. Fauna of Waters in Deserts

Conditions of life in a permanent well or spring in the desert, or in a river which runs for part of its course through desert, are not in any way different from those which prevail in similar situations elsewhere, and the animals of these springs and rivers do not concern us. But there are other and more temporary water-places in deserts, and those of them which are liable to be filled with water at fairly regular intervals support a very interesting fauna.

The inhabitants of the temporary pools are exposed either to death or else to the full rigour of the desert climate for many months on end, while the pools are dry; and even when they are filled with water the position of the animals is precarious, because the period which they will be able to devote to active life, to feeding and to reproduction, is a short one. Moreover, during the gradual drying up of their pool the saltness of the water increases: so that the animals are faced with three separate problems—the ordinary problems of life in fresh water, the gradually increasing salinity of their water, and its eventual disappearance.

Certain groups of animals, abundant in the fresh water of other climates, are entirely unable to solve these problems. The Newts, for instance, are found all over Northern Europe and Asia, but they are limited in a southward direction by the northern edge of the Great Palæarctic Desert, and no newt appears to have penetrated or crossed it. It would

be interesting to study the effect of belts of desert upon the distribution of leeches, planarians, and other naked damp-skinned animals.

Other animals are unable to survive the desiccation, but become temporary colonists of water-holes in deserts and when the water dries up are locally exterminated. Among them are denizens of permanent waters, which are occasionally introduced into a temporary pool by floods; this is an accident of common occurrence to small fish, and doubtless to a large number of other forms of life. Winged insects also, whose early stages are passed in waters, frequently colonize these temporary pools. This temporary colonization is of course most commonly seen in parts of the desert close to permanent pools or rivers: temporary pools in such places are invaded by many forms of gnats and mosquitoes, by gad-flies (Tabanidæ) and by dragon-flies. It is probable that the Tabanidæ and dragon-flies seldom pass successfully through their early stages, which are of long duration; but the gnats and mosquitoes frequently pass rapidly through several generations. As the pool shrinks in size and increases in saltness it becomes a fit home for the larvæ of small flies of the family Ephydridæ, and these are sometimes present in enormous numbers.

But it is the permanent inhabitants of these temporary pools which are most interesting, because their methods of solving the problems which confront them are so varied. The Phyllopod Crustacea (e.g. Apus and Estheria) exist through the drought as eggs, and can survive a period of drying which

extends over years. Recurring periods of drought are necessary for their existence, so that it is not remarkable that they should be found in deserts and semi-deserts in nearly every part of the globe. One member of this group, the Brine Shrimp (Artemia), is not only extremely resistant to drought in the egg stage, but also requires for its development water nearly or quite saturated with salt; and it is found in temporary salt pools in many parts of the world, both in deserts and other situations. Certain Phyllopods are capable of extremely rapid growth when the mud in which their eggs have been dormant is flooded, and when the shallow pool is heated by a desert sun. Spencer records that Apus in Central Australia reaches a length of 2½ inches in fourteen days after rain falls.

Other inhabitants of temporary pools descend into the mud when the pool dries up, and there continue to exist. Examples are the crab (Telphusa) and crayfish (Astacopsis) of Central Australia, and many water-beetles and molluscs. Of the Gasteropod molluscs many are protected by an operculum, with which to close the mouth of the shell: *Isidorella newcombi*, in water-holes in Central Australia, plugs the shell with mud, which is probably specially prepared by passage through the alimentary canal.

The biology of the frogs found by the Horn Expedition to Central Australia has been treated at some length by Spencer. Among the species collected were some which showed marked ability to breed rapidly and take advantage of a short favourable period, and others whose habits enabled

them to survive drought in a remarkable manner.

That frogs are able to exist at all in temporary waters in Central Australia is very remarkable, because their need for water is great, and their damp skins are entirely unsuited to life in a dry atmosphere, in which they invariably die. Six species were found in the desert region, but two were rare and little was discovered about their habits. The remaining four all showed different interesting methods of overcoming the hostility of their environment. They were all of them able to spawn at any time of year, as soon as rain had fallen.

Hyla rubella, a close relative of the green Treefrog of Southern Europe, was found in nearly every water-hole which was visited during the dry season. It appears that it does not burrow in damp soil, and therefore when its water-hole dries up it perishes. On the other hand, it is a very rapid breeder, and if rain falls heavily its tadpoles are carried down the channels and its range is, for the moment, very greatly increased. It is therefore a species which depends for its success in colonizing Central Australia on its ability to produce its young rapidly and in large numbers: it might be said to be successful because its high birth-rate after rain exceeds its high death-rate during the dry weather. If the drought exterminates a colony of this frog at a certain water-hole in the bed of a stream, the next flood will enable the species to colonize the same spot once again from a permanent pool.

Another common frog was *Limnodynastes ornatus*. Like many of the frogs of the more arid parts of

Australia this species is able to excavate burrows in soft soil. These it makes in sandy places in the beds of temporary streams, and it reaches a layer of damp sand even though the stream has been dry for a long time. The burrows are not permanent; a fresh one is made for each day, and at night, when the temperature is low and the humidity high, the animal ascends to the surface to hunt for beetles.

Heleioporus pictus is another burrowing form, but it makes permanent burrows. In these it exists for months at a stretch during periods of drought. I am informed that the eggs are laid in the burrow, about 18 inches deep in the sand, in a foamy mass. Development occurs in the egg to such a stage that the tadpole is ready to emerge as soon as rain falls. The albumen of the egg is hygroscopic, and when moisture is abundant it is absorbed in such quantities as to burst the membrane which covers the egg, and release the tadpole.

Chiroleptes platycephalus resembles the last species in making a permanent burrow and in its ability to exist in it through a long period of drought. It possesses also remarkable powers of storing water, and it can contain a very considerable quantity in its urinary bladder, subcutaneous tissues, and peritoneal cavity; when it is fully charged with water it is almost spherical. It makes permanent burrows to the depth of about a foot in soil which will shortly be baked by the sun into a mass of hard clay, and here it remains for the dry season. By means of its burrowing and its powers of storing fluid it is able to resist long droughts; permanent springs and

pools are unsuited to it, and it is only found in places in which it will be exposed to desiccation periodically. This animal can contain so much fluid that it is occasionally used by the Australian aborigine as a source of drinking-water. It appears to imbibe the water through its skin, as well as its mouth, and to do so very rapidly; an Australian friend, Mr. L. Harrison, writes to me that if you "put a lean, dry, herring-gutted Chiroleptes into a beaker with 2 inches of water, in two minutes your frog resembles a somewhat knobly tennis-ball."

iii. Heat and Relative Humidity

These two factors must be considered together because under natural conditions a high temperature and a low relative humidity are generally associated (page 23). It is not therefore possible, in the absence of experimental work, to discriminate between the effects of the two.

The very existence of small animals on the surface of the desert at midday is remarkable. Most of these animals—for example, the lizards and beetles—are cold-blooded, so that one supposes that their temperatures approximate to that of the air in which they find themselves at any given time; and as they are relatively small the fluctuations of their internal temperatures must be rapid. In spite of this, animals do manage to exist on the desert soil even in the middle of the day in summer.

Good examples among the reptiles are the Agama lizard at Ur of the Chaldees, to which reference has been made (page 92), and the Chuckwalla (Sauro-

malum), a vegetarian lizard of the Californian deserts which sits upon rocks when they are too hot for the hand to touch (Camp).

Many insects have the same power of living on the surface of the soil at midday, even during the hottest season. On June 2, 1922, I observed at Jericho, Palestine, at noon that the shade temperature was 90° F. (32·3° C.), and the surface of the hard clay soil 124° F. (50·8° C.), and on it two species of mantis larvæ (Eremiaphila and Fischeria), and adults of a Short-horned Grasshopper, were moving about. In deserts nearer the Equator much greater surface temperatures (page 21) are attained, but these figures serve to show the degree of heat to which the insects, etc., are exposed on the bare desert.

The case of the diurnal mammalia of the desert is very different, and their survival of summer midday conditions is not so remarkable. Such animals as hares, gazelles, and camels are large, so that in any case they would not be exposed to very rapid fluctuations of internal temperature: they are, moreover, warm-blooded, that is to say, provided with a mechanism which maintains their bodies at or near a constant temperature: therefore fluctuation of air temperature affects a gazelle or camel, or even a hare, very much less than it affects a lizard or beetle; so that the power of the mammals to survive the midday heat is less remarkable than their ability to provide themselves with water, by the evaporation of some of which they maintain their "normal temperature."

On the other hand, to many desert-dwellers exposure to the climate at midday is very rapidly fatal. The Horn Expedition to Central Australia observed that if the lizard Tiliqua was taken from its hole and put on the sand at noon it ran a few yards and rolled over dead, and similar examples might be multiplied. The animals which are unable to survive surface conditions at midday resort to various devices in order to reach a more equable temperature and humidity than is prevalent in the open air. A few birds obtain all the shelter they require by getting into the centre of trees and bushes. Thus in the plain of Jericho the Great Grey Shrike (*Lanius excubitor aucheri*) and the black and white Wheatear (*Saxicola lugens*) take refuge during the heat of the day in midsummer in the bottoms of bushes of Atriplex and Zizyphus (Fig. 25). At all other times they are most conspicuous birds, the Shrike perched on the top of a Zizyphus, and the Wheatear in any unprotected position. In a similar way one may observe House Sparrows (*Passer domesticus biblicus*) and White-cheeked Bulbuls (*Pycnonotus leucotis mesopotamiæ*) bury themselves during summer days at Basra in the dense mass of leaf-bases and young shoots which spring from the crown of a date-palm.

Many small animals take refuge under stones and in similar places, particularly at the seasons when traces of moisture are still present. In the Great Palæarctic Desert, wherever mixed stones and earth occur (page 47), a large collection of small animals may be obtained by turning over stones during the

spring and early summer. One obtains such creatures as woodlice; millipedes and centipedes; spiders, scorpions, mites and pseudo-scorpions; lepismids, Japyx, earwigs, cockroaches, crickets, very numerous beetles, bugs, ants; snails and occasionally slugs, and earthworms. What befalls these animals in the hot and dry season is largely a matter of conjecture. Probably some descend deep into cracks in the soil, and others æstivate in the egg and possibly in other stages. Spencer attributed the existence of land-snails in Central Australia to various factors in different species. Some existed on the shady side of hills, others æstivated among tree roots, others closed the mouth of the shell with a plug of mud; others again were minute and descended deeply into the clefts in the soil. It is at any rate certain that the rich fauna that one finds under stones in Persia, Palestine, Algeria, and other stony deserts, in springtime is almost as ephemeral as the annual flowers, and it is very remarkable that such moisture-loving forms as snails and earthworms should be able to exist through the summer in any stage in these countries.

The geographical distribution within the Great Palæarctic Desert of these multitudes of small creatures depends among other factors on the presence of stones under which to shelter, and of regularly recurring rainfall, but a very similar association may be found in Lower Mesopotamia, a stoneless plain consisting of nothing but the finest silt carried down by the Tigris and Euphrates; in this country

a fauna is found after rain, between the trunk and the leaf-bases of the date palm ; this fauna is relatively rich and contains all the groups which I have just enumerated as characteristic of stone and earth desert in spring. In fact, one may say that the animals which shelter in the date-palm in Mesopotamia are the biological counterpart of those found under stones in Persia or Palestine. To what extent the same genera or species of animals are represented in both we do not at present know.

Other animals which are unable to endure the climate of the surface of the desert dig burrows or use burrows which have been excavated by other creatures. They thus easily reach a zone in which temperature and humidity are nearly constant (page 22). In the group of active burrowers fall certain lizards and snakes, and nearly all the small rodents (Jerboas, Gerbils, Spiny Mice, and many others), and some at least of the small marsupials of Central Australia. Many observers have noticed the extraordinary ability of the House Mouse (*Mus musculus*) and its very close relatives (*Mus gentilis* and other forms) to colonize human habitations in nearly every part of the Great Palæarctic Desert : the rapidity with which they become abundant in isolated camps in Mesopotamia was frequently noticed. These animals are protected from great fluctuations of heat and relative humidity by their burrows which are made beneath houses, and because they frequently travel from place to place in boxes and bales. If they were diurnal and lived openly in man's habitations they would be faced

Fig. 38.—Holes of *Dipodomys deserti* in Sandy Ground, Mellen, Arizona. (*Photo:* Dr. J. Grinnell, Museum of Vertebrate Zoology, University of California.)

with such fluctuation of temperature and humidity as might prevent their colonizing houses in the desert.

Many of the small wild rodents close the mouths of their burrows by day with a plug of earth, and no doubt this tends still further to stabilize the climatic conditions which prevail in the burrow. Detailed observations on this point are lacking for many species, but among rodents which plug the burrow one may mention *Dipodillus dasyurus* and *Jaculus loftusi* and *Nesokia buxtoni* in Mesopotamia, and the American genus Dipodops; among those which leave the burrow open are Jaculus (species ?) in Palestine, and *Dipodomys deserti* (Fig. 38) in the American deserts. That the conditions in a burrow are widely different from those which prevail outside is sufficiently shown by Pitman's observation on the Jerboa, *Jaculus loftusi*, in Lower Mesopotamia. This species is absolutely nocturnal. "Their earths go steeply into the ground for 2 or 3 feet and the little creatures evidently lie up all day in the cool, damp earth as I always noticed that captive specimens, of which we tried to keep many from time to time, suffered tremendously from the great heat during the day, even when kept in the coolest of places dug right into the ground, so much so that we never managed to keep any alive for more than a few days."

Among the burrowing insects one must mention two groups, the Crickets and the Ants. Species of Cricket (Gryllidæ) are often found even in the more barren parts of the Great Palæarctic Desert;

they take refuge by day in burrows dug under stones, and issue forth at night when the air is cool and the humidity not very low: the ants have successfully overcome the climatic difficulties, and a number of species may be found in the Great Palæarctic Desert and in Central Australia; many of them come up from their subterranean nests in the morning and late evening, but others are active during the heat of the day.

In the group of animals which uses burrows constructed by other animals are included the majority of desert snakes and lizards (at any rate in the Great Palæarctic Desert) and a number of nocturnal beetles (especially some Carabidæ and such Tenebrionidæ as Blaps).

Many larger creatures, whose powers of movement enable them to rest at some distance from their feeding-grounds, take refuge in caves. Conditions in a cave differ fundamentally from those prevailing in the open desert: in the cave, temperature is nearly constant, humidity is more constant and higher than in the desert, and light is absent (C. B. Williams). But for the presence of caves the existence of bats in desert areas would be impossible, but in deserts in which caves occur, particularly if drinking-water is available, bats are frequently numerous, both as species and as individuals. Birds which nest or which roost in caves are quite an important element in the fauna of the Great Palæarctic Desert: examples are sub-species of the Eagle Owl (*Bubo bubo*) and Little Owl (*Athene noctua*), and of the Swifts (*Cypselus apus*, *C. murinus*,

and *C. affinis*), and of the Rock Dove (*Columba livia*).

None of these sub-species are very highly modified for life in the desert, and the species from which they are derived are distinguished for their ability to live in many types of climate and country; in fact, the two owls, the dove, and the Common Swift all breed as far north as Northern Europe. It seems that the presence of caves, with their relatively unvarying temperature and humidity, may have enabled these vigorous and adaptable species to penetrate a short distance into the desert. Certain of them now breed and roost in houses and ruins, but this is clearly only a slight extension of the cave-haunting habit.

It is probable that a closer study of the cave fauna in such countries as Egypt and South Palestine would reveal most interesting forms of life. The contrast in climate between open desert and cave is so great that the colonization of the cave by animals which are specialized to live in the surrounding desert would present great difficulties.

The eggs of birds which breed upon the surface of the desert and are exposed to its summer climate are in a position of great danger, because if they are left uncovered by the parent birds they are rapidly killed by the heat during the daytime. It should be remembered that, at any rate in the Great Palæarctic Desert, most of the birds breed during the hot weather, e.g. Sandgrouse (page 85), Common Pratincole, and others. It is only the largest of eggs, those of the ostrich, which can

survive prolonged exposure to the desert sun. Though it is extremely difficult to disentangle truth from fiction in the case of the wild ostrich, I think that the following facts are now established. Neither in Africa nor in Arabia do ostriches bury their eggs in the sand, as is frequently stated. The eggs are often left entirely uncovered and exposed to the heat in the middle of the day, particularly in the hotter parts of the bird's range. At other times of the day, and particularly in the colder parts of the bird's range, the eggs of the ostrich are incubated by both parents in turn.

Smaller eggs, which are more rapidly penetrated by heat, are quickly killed under conditions which merely serve to incubate the great eggs of the ostrich. The existence of this danger was clearly demonstrated during the fighting round Kut el Amara, and in other places in Mesopotamia, where many eggs of Sandgrouse were destroyed by the sun because the parent birds were driven from their eggs by gunfire.

C. B. Ticehurst tells me that such eggs as those of *Geochelidon nilotica*, *Glareola pratincola*, *Sterna caspia*, and *Larus gelastes* are killed by exposure to hot sun. These birds are not desert breeders, but nest upon mud-banks under conditions which frequently approximate to true desert during the breeding season, and his observations are therefore pertinent.

The devices to which the parent birds resort to avoid such fatalities are extremely interesting because they are so varied. Many desert breeders

place their nest as far as possible under shelter, most Larks under a small bush, all Wheatears in a hole or small cave, Hey's Partridge and See-See (Ammoperdix) in holes in small cliffs, or under boulders. Of the birds which breed in the open without protection from rocks or bushes, most species sit upon the nest from the time the first egg is laid. The eggs are therefore kept at a nearly constant temperature by the bird's body, and are not exposed to the heat by day and the cold by night. It appears to be established that Sandgrouse incubate from the time of laying the first egg, though Meade-Waldo's observations in an aviary in England do not support this view.

It is recorded that the Pratincole (*Glareola pratincola*) stands over its first egg, and by doing so protects it from the sun's rays, and that a small Tern (*Sterna saundersi*) which breeds on the bare shore at Karachi (Sind) does the same.

After incubation has commenced the majority of desert birds are unwilling to leave their eggs, and if they are compelled to do so they return to them as quickly as possible. This has been noticed by several observers of the Courser (*Cursorius gallicus*) and Sandgrouse. The eggs of the Sandgrouse have additional protection from heat, for when one parent returns from watering, and relieves the other from the duty of incubation, its breast is saturated with water. Therefore it appears that the eggs and the soil on which they are laid are wetted every day, which must tend to prevent overheating.

The effect of the wind upon the flora indirectly affects the fauna. To the plants it is harmful both by reason of the physical damage done by violent gusts and wind-blown sand and small pebbles, and also because it rapidly dissipates the slightly moist air which accumulates round the plant owing to transpiration. Increased transpiration results, that is to say, increased loss of water which is already very scarce : it follows that plants may be able to exist on a specified amount of water if they are protected from wind, and may be killed if they are exposed to the wind.

This is well seen wherever a wind of constant direction blows through a narrow valley ; any large rock which breaks the force of the wind, and thereby reduces evaporation and transpiration under its lee, shelters a richer flora than will be found elsewhere.

It is in fact true that places exist which are desert primarily because of wind. For instance, throughout great parts of the Libyan Desert the distribution of plants is determined rather by the presence of shelter from wind than by any other influence.

The effect of a strong wind loaded with sand upon the very scanty spring vegetation on the Libyan border of Lower Egypt is thus described by Thomas. "On April 13, towards the close of the growing period of most plants, a hot wind blew in from the desert for about five hours, raising great clouds of sand which drove along the surface of the ground like mist. The temperature went up considerably, in spite of the sun being obscured, and was over

45° C.: the air felt intensely dry and was charged with sand-grains which produced a smarting effect on the exposed skin. The wind went down during the night, but it remained hot and no dew fell. The storm continued in this way for the next two days, and its effect on the vegetation was very striking. All flowers and young parts of plants had shrivelled, the upper portions of the green branches of Calligonium had died and had often been broken off, the fruits of this plant had dried and had become quite hard: most of them were detached from the plants and were blown about in all directions. The upper portions of the stems of *Heliotropium luteum* were withered and dead, and had lost all the younger leaves. All the plants appeared very much withered, except *Imperata cylindrica,* which seemed untouched. Many plants seemed partially uprooted, especially Pulicaria and Polygonum; in reality the wind had removed the surface layers of the sand round them, and 20–25 cm. of rootstock were exposed—this showed the importance of being deep-rooted. The surface roots of *Panicum turgidum* were very frequently laid bare. In other cases plants were wholly or partially buried."

The direct effect of wind upon the animals, especially the smaller animals, also merits discussion, as it has apparently caused modification of habit in some animals and of structure in others. Certain small Blue Butterflies (Lycænidæ) which inhabit the Great Palæarctic Desert possess the power of continued flight within one small bush, from the shelter of which they seldom issue. Butterflies of

the genus Tarucus may be observed flitting up and down continuously inside a bush of Zizyphus, without leaving the middle of the bush, and sometimes continuing in flight for many minutes. The minute *Chilades galba*, another member of the same family, is able to limit its flight within a plant of Ononis (" Rest Harrow "), which is only a foot in circumference, and to remain on the wing in this little bush, when such a wind is raging outside as to prevent the flight of all other butterflies.

Another interesting modification of habit has been observed by Hartert, Rothschild, and others in the Algerian Sahara. The prevalent wind is from the east, so that the sand and debris which it carries settle on the west side of any bush or stone, because relative calm prevails under the lea of the bush. Several species of Passerine birds regularly make their nest against the windward side of small bushes, and so avoid being smothered with sand and debris. They then fortify the outer side of the nest with a mass of pebbles, apparently in order to protect the nest from wind. This seems to be the invariable habit of Clot-bey's Lark (*Rhamphocorys clot-bey*), which collects pebbles weighing as much as half an ounce. In the Larks *Ammomanes phœnicurus arenicolor* and *Eremophila alpestris bilopha*, the habit of placing the nest on the windward side of a small bush is apparently universal, but the barricade of stones is occasionally very small or quite absent. The nests of the Trumpeter Bullfinch (*Erythrospiza githaginea zedlitzi*) are invariably on the windward side of small bushes, and perhaps protected by their position

immediately under the bush, for they were without a barricade of stones. One species of Wheatear (*Saxicola leucura*) has a similar habit, nesting under a rock and almost blocking the passage to the nest with a mound of pebbles: the bird does this in the Algerian Sahara, and also in the Sudan. Another Wheatear (*S. leucopyga œgra*) shows what is probably a development of the same habit, for it nests in holes in rocks and crevices in walls and constructs a wide path of flat stones up to the mouth of the crevice.

Similar habits have been observed in other countries, but no information is given as to the direction of the prevalent wind, or the side of the bush under which nests were habitually built. In the Sudan Chapman has recorded the building of barricades by an Ant-Chat (*Cercomela scotocerca*) and a Lark (*Ammomanes deserti*), and states that the Cercomela collects as many as 130 pebbles in its barricade. This habit is the more remarkable as it has been developed by birds which are not closely related to one another; one presumes that it has originated independently in the Finch, in the Wheatears and Ant-Chat which are closely related, and at least once among the Larks.

Of modifications of structure which are apparently induced by the wind, the most striking is the winglessness of many insects whose near relatives in other types of country are winged. In the order Orthoptera one may observe several series of insects in which the wings are progressively reduced. Some species have the wings so shortened that they are useless for flight, but normal in structure and

proportions; in others they are present as minute vestiges, or so reduced that their sole function is to assist in the production of the insect's chirrup. In some species the reduction has proceeded much further in one sex than in the other. Short-winged forms may be observed in the Long-horned and Short-horned Grasshoppers, in the Mantis family, and in the Crickets, so that they must have arisen independently many times in the Orthoptera. The phenomenon is not by any means confined to desert species, but is much more frequently seen in them than in those of other environments. For instance, in Algeria and Tunisia about half the Orthoptera are wingless, even when the forms which inhabit the fertile coastal region are included in the count.

Among the Coleoptera (Beetles) fusion of the wing-cases and consequent flightlessness is a character of very many Tenebrionidæ (Fig. 42, facing p. 150) and Carabidæ (Ground Beetles) in deserts. Loss of the power of flight in these two families of beetles and in the Orthoptera is not confined to species which inhabit deserts, but is much more common among them than among others. That it is due solely to the wind and not to any other influence is apparent from the fact that a similar loss of the power of flight occurs in many other environments which are exposed to violent winds, but do not in any other respect resemble deserts: the insects of mountain tops and of small isolated islands furnish examples.

The dispersive effect of the wind upon small animals can be exercised in the absence of any modi-

fauna of sandy desert. To that, therefore, I propose to confine our attention entirely.

It has been shown (page 40) that sand probably presents more difficulties to the desert flora and fauna which attempt to colonize it than does any other type of desert. It is not, therefore, to be wondered at that the fauna of sandy areas, and particularly of areas in which the sand is loose, is a small one, and that it consists largely of animals which in overcoming the difficulties of life in sand have become unfitted for life in any other environment.

Grinnell has described the conditions of life of certain species of sand-living rodents in the North American deserts. The Round-tailed Ground Squirrel (*Citellus t. tereticaudus*) requires large areas of sand, and also bushes, under which it can burrow : it is frequently abroad in the daytime, but it avoids direct sunshine by passing rapidly from the shade of one bush to that of another. It cannot endure the fierce heat of midday on bare sand, and if an individual is caught in a trap uninjured but exposed to the sun's rays it dies quickly. This rodent is therefore an animal which requires the co-existence of a geological and floristic factor, in order to enable it to live in a particular place. The Big Desert Kangaroo Rat (*Dipodomys deserti*, Fig. 38) lives in the same sandy places as the Round-tailed Ground Squirrel, but its requirements are quite different. It is nocturnal, and is sheltered in its burrow from the conditions which prevail during the day ; it is therefore indifferent to the presence of bushes.

What it requires is blown sand which must be at least a foot deep. The probable explanation is that sand is the only soil in which it is able to burrow; for its incisors are weak, and its claws and feet small. In fact, what determines the presence of this rodent in a given spot is the coexistence of two physical factors, loose sand for its burrows, and sufficient depth of sand to accommodate it.

Associated with the Big Desert Kangaroo Rat, and largely dependent on it for food, one finds the Kit Fox (*Vulpes macrotus arsipus*), which is a purely desert animal and apparently occupies the same place in nature in the American sandy deserts as the Fennec Fox in Africa. The Fennec Fox (*Vulpes zerda*) lives exclusively in sandy places in the Sahara and Egypt; it is a small, rather weak fox, which feeds upon beetles, grasshoppers, vegetable matter, and a few small rodents.

The Marsupial Mole (Notoryctes) of Central Australia is an inhabitant of sandy places. It possesses the general outward form of our own Mole (Talpa), and of other burrowing mammals, to none of which is it in any way related. It is a cylindrical animal, with strong shovel-shaped feet, and a reduced tail, and it has no eyes. It makes no definite runs, because the sand collapses at once after its passage, but it spends its time pushing through the sand in search of insects, particularly ants. The Tuco-tuco (Ctenomys), a rodent of South America, exhibits many of the external characters of the mole, though it is related neither to the mole nor to Notoryctes. It is found in isolated colonies wherever sandy

patches occur in the pampas and semi-deserts of South America, and there is a tendency for the individuals of each colony to differ in colour, size, and other characters from those of other colonies.

The reptiles found in sand are peculiarly interesting because they show many examples of convergence. Camp, in describing the habits of the reptiles of South-Eastern California, states that in one burrowing snake and three lizards the rostrum is specially developed, protruding beyond the mouth. These lizards belong to several different families, so that this similarity in the rostrum is due to convergence and not to close relationship.

The same enlargement of the rostrum has been recorded by other authors in several different genera of snakes which burrow in the light soil or sand of arid regions: rather similar are the fringed scales surrounding the eye in some sand-dwelling lizards. In the Jerboa (Jaculus) the muzzle can be contracted and the nostrils narrowed and almost covered by a fold of skin. It appears that the function of this is to protect the nostrils when the animal is burrowing and pushing soil with its broad snout (Anderson and De Winton, and Pocock).

Certain lizards and snakes possess the power of burrowing into sand with extraordinary rapidity. The lizards which do so do not use their legs, but progress by rapidly bending the body from side to side. In members of the Skink family (Scincidæ) in North African deserts this is associated with progressive reduction of the limbs, and members of this family exist showing various stages from the normal

complement of four legs to complete absence of limbs.

Many lizards living in sandy places are extremely rapid in their movements. When they are not running they stand alert with the head held high and the front part of the body raised on the fore-legs, and when they are in motion the tail is held well above the ground as a counter-balance. This holds good of lizards of several families, from several parts of the world; and the species which are predaceous and those which are preyed upon both exhibit it. In many of them the toes of the fore- and hind-feet are broadened by a fringe of elongate scales. Apparently all of these species live on sand, some of them on great stretches of dune, others on the small heaps of blown sand which accumulate under bushes in deserts of mixed stone and earth: it seems legitimate to conclude that the fringe widens the surface, which presses on loose sand and acts in the same way that a snow-shoe does on loose snow. As Figs. 39 and 40 show, these fringes are developed in several families of lizards, in deserts in different parts of the world. Of the seven genera figured Phrynocephalus (A) is an Agamid from Transcaspia; Acanthodactylus (B) and Scaptira (C) are Lacertidæ, distributed in the Great Palæarctic Desert; Callisaurus (D) is an American Iguanid; Teratoscincus (E), Stenodactylus (F), and Ceramodactylus (G) are Palæarctic desert-living Geckonidæ. It is clear that this curious character has been developed on at least half a dozen different occasions, and it is clear also that it is a response to life on sand. I am most grateful

to Miss J. Procter, of the British Museum (Natural History), for her kindness in selecting these most interesting lizards.

Among the insects, the ants which live in sandy

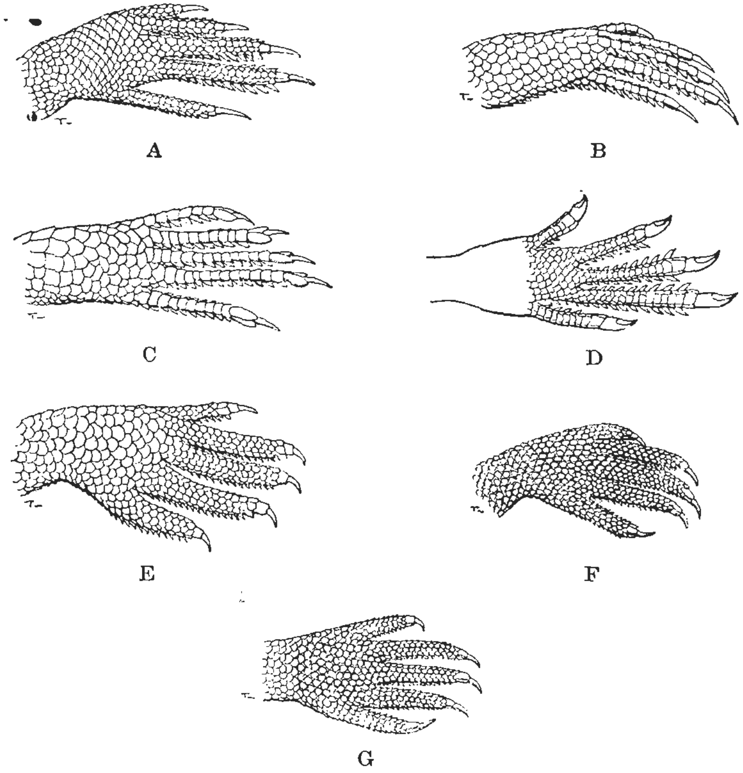


Fig. 39.—Fore-feet of the following Lizards:—A. *Phrynocephalus mystaceus* (× 1½). B. *Acanthodactylus scutellatus* (× 2). C. *Scaptira grammica* (× 2). D. *Callisaurus (Uma) scoparius.* After Cope, "Amer. Nat.," 1894. E. *Teratoscincus scincus* (× 2). F. *Stenodactylus guttatus* (× 3). G. *Ceramodactylus doriæ* (× 3).

and dusty places are remarkable. In very many of them a "circum-oral crate" of stiff bristles is developed upon the structures which surround the mouth. The purpose of this is clearly not connected

with feeding, for it is well developed in harvesting species, in predators, and in honey-pot ants (page 72).

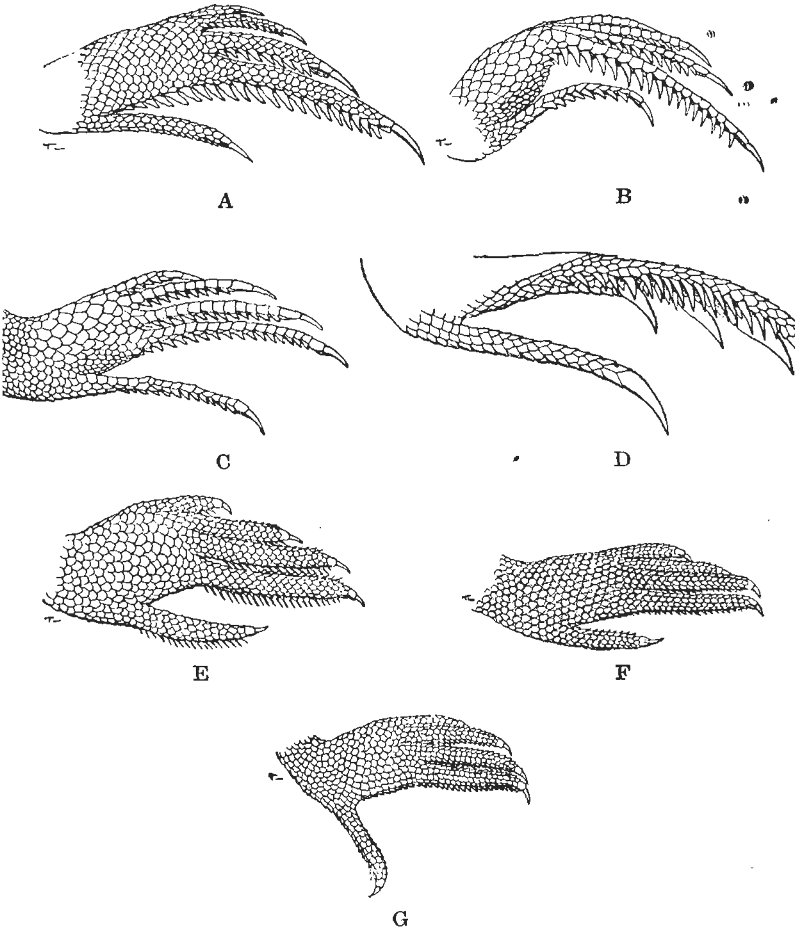


FIG. 40.—HIND-FEET OF THE FOLLOWING LIZARDS :—A. *Phrynocephalus mystaceus* (× 1½). B. *Acanthodactylus scutellatus* (× 2). C. *Scaptira grammica* (× 2). D. *Callisaurus* (*Uma*) *scoparius*. After Cope, "Amer. Nat.," 1894. E. *Teratoscincus scincus* (× 2). F. *Stenodactylus guttatus* (× 3). G. *Ceramodactylus doriæ* (× 3).

Wheeler suggests that it is used to clean the strigil on the fore-leg, which in turn is used for cleaning

the antennæ, etc., and that it is only developed in ants from sandy and dusty places because the strigil is peculiarly likely to become clogged in such places.

The protozoa of the sand in the neighbourhood of Cairo have been investigated by Thomson and Thomson. These microscopic animals exist in the dry sand in a resistant envelope or "cyst," from which they only emerge when the sand is moist, and as it dries they again envelop themselves in "cysts." In the climate of Cairo their period of activity is reduced to a few days a year, and their period of dormancy is extremely protracted. They are exposed to light and heat and drought in the sand, and yet the investigators were able to recover about fifty species from the sand after eight months of drought. Most of them belonged to forms known elsewhere from fresh water; that they were dependent on occasional moistening is shown by their great rarity in the sand of Luxor in Upper Egypt, in an area which is without rain in the average year.

CHAPTER VI

RELATIONS BETWEEN ANIMALS AND PLANTS

Interrelationships between animals and plants may be divided into that class in which the animal is dependent on the plant, and that in which the plant depends upon the animal. The first group of relationships is the larger, in deserts as in other types of environment. All the world over it is true that the animal depends on the plant for compounds of nitrogen and compounds of carbon: most of the essential food of every living animal comes directly or indirectly from plants, and with it the animal swallows a proportion of water. The plants also fulfil certain subsidiary functions with regard to the animals; they furnish them with shelter from the elements, and protection from enemies. One may therefore say in general terms that the plant provides the animal with food and water, and with shelter and protection.

It is convenient to consider at one time the food and the water which animals in deserts derive from the plants which they eat. The food and water are swallowed together, and may for the moment be regarded as a single contribution made

by the plant kingdom to the animals. It must be remembered that in the desert this source of water is of much greater importance than it is under other conditions. In most environments the water which is part of the food material is incidental: in the desert it is essential, and commonly the only available supply.

We have already (Chapter III) divided the desert flora into three biological groups—the annuals, the perennials which lie buried during the unfavourable season, and the perennials which exist above the surface of the ground at all seasons. Let us see how each of these groups is used by the animals as a source of food and water.

The conditions which are best for the annuals, and which lead to the production of abundant annual vegetation after rain has fallen, are favourable also to many animals. No sooner have the young annual plants appeared above the earth than they are attacked by numbers of caterpillars, bugs, leaf-eating beetles, wood-lice, and other plant-eaters: as soon as the blossoms open they are visited by bees, butterflies, moths, thrips, flower-eating beetles, and many other small creatures in search of nectar or pollen or petals. For a very short time the climate and the floral environment is favourable to insects in general. Then the soil dries, the air becomes hot, and most of the flowers and insects disappear.

The majority of insects which are dependent on the annual vegetation in the Great Palæarctic Desert are active for a very short period and exist through the dry nine months of the year in a state

of dormancy, some of them as pupæ, others as eggs, others probably as resting larvæ. A few species prolong their season of activity and produce a series of broods by utilizing first one food plant and then another, as the plants successively become available. A good example is furnished by *Papilio machaon*, the Swallow Tail Butterfly, in Mesopotamia. In April and May it fed on the flowers of *Ruta tuberculata*, and as this plant began to go to seed *Ammi majus* came into flower, and became for the moment the plant on which eggs were most commonly laid. This plant was followed by *Ducrosia anethifolia*, which was not common, and probably not an important food plant. While *A. majus* and *D. anethifolia* were running to seed, *Ammi visnaga* flowered and became an important food plant; it was in full flower in June after the first three were quite dry. A fifth plant, *Fœniculum vulgare*, was also found to be eaten by the larvæ of *P. machaon*. It seems then in Mesopotamia that the Swallow Tail Butterfly has a regular succession of food plants belonging to two unrelated natural orders of plants—the Ruta to the Rue family, the others to the Umbelliferæ (Peile). One might argue from this that if a caterpillar or other plant-eater possesses the power of living on a variety of plants it may be able to survive under conditions which would exterminate another caterpillar that could only feed on one plant: in fact, that polyphagy may be one factor determining the survival of certain species in the desert.

In rather a similar way I noticed in Mesopotamia

that a very large number of species of bees, fossorial wasps, ruby wasps, and true wasps congregated at whatever plant was in bloom. The Hymenoptera could not afford to indulge their preferences; every species which was on the wing might be taken now in a field of beans in flower, a few weeks later at Zizyphus blossom, or Acacia (Prosopis), or Lycium; many of the species remained on the wing during long periods, and a particular species might frequent half a dozen different flowers, each one exclusively for a short season. Such a thing does not, I think, happen in lands where flowers are commoner and the flowering season is more prolonged.

The inroads upon the annual vegetation of the larger grass-eating mammals, for instance, the gazelles and hares in the Old World, are relatively unimportant because the numbers of these animals are limited by the scarcity of fodder during the dry season. Spencer showed that adults of the marsupial *Phascogale cristicauda* in Central Australia were 40 per cent. to 60 per cent larger at the close of a good season following rain and plenty of vegetation, than they were in a season in which rain had been deficient. He believes that this explains the great variation in size which may be observed among adults of other species of small marsupials. It is only such small beings as the insects, with their power of lying dormant in unfavourable seasons and of rapid multiplication, which can take advantage of the annual flora of the desert.

The plants of the second biological group, those

which store food in bulbs, tubers, and other structures underground, and are only above ground for a short season, are probably of considerable importance to the fauna, but we have little actual knowledge on this point. Tristram, in speaking of the deserts of Southern Palestine, says: "The vast number of little rodents in apparent deserts is explained by the nature of their food, which is chiefly supplied by bulbous roots. The greater part of the desert plants are tuberous or bulbous, and after nine months of utter barrenness, the first winter rains soon carpet the waste with a brilliant spangling of bulbous flowers—crocus, iris, squills, asphodels, cyclamen, and others. Their glory is soon over; but the large succulent roots remain, retaining their moisture through the summer, and affording abundant nutriment to the little burrowers." Hart states that the wild boar wanders far out into the semi-deserts of Beersheba in order to root for bulbs, particularly those of the great squill (Urginea, Fig. 26), and that in consequence roots of this plant become quite difficult to obtain. In the burrow of a Mole-rat (Spalax), in Egypt, Anderson found a store of sixty-eight bulbs, but he does not state the species of plant to which they belonged.

It is natural that animals should be particularly associated with plants of the third group, which are above ground at all seasons of the year, and which supply food and water even at unfavourable seasons to the creatures which can make use of them. Many examples might be found of mammals and

birds which subsist largely or entirely on some particular desert perennial. In Mesopotamia we observed a very close relationship between the salt-loving bush (Suæda) and a Dwarf Gerbille (*Dipodillus dasyurus*). The Suæda was a bush about 3 feet high and grew in salt patches in the desert: a few bushes of Atriplex and Salsola were the only plants found associated with it, and they were not common. Several insects lived on the Suæda, and the Dwarf Gerbilles lived on any insects they could catch, and on the succulent leaves of the plant. They required no water in captivity, and in nature they and the Suæda bush lived far from the River Tigris: there is little doubt that they were entirely dependent on it, and the insects found upon it, for food and water. The desert was flat and composed of silt: it was devoid of any form of shelter except the Suæda bushes, and among its roots the Dwarf Gerbilles made their burrows. We may therefore suppose that they derived from the plant not only food and water but also protection from the foxes and occasional jackals which existed in those parts of the desert. So far as I know only one other mammal, a hare (*Lepus connori*), occurred in the salt patches of desert where the Suæda flourished. It is natural that the animals should be few in a place where only one plant grows and no water can be obtained except from the plant, and it is noticeable that three of the four mammals, the fox, jackal, and hare, are active cursorial forms able to wander far from the Suæda patch in search of water and food.

In the same way it is stated that Pallas' Sand-grouse (*Syrrhaptes paradoxus*) feeds very largely on a salt-loving desert Chenopodiaceous plant, Agriophyllum, in Central Asia.

Such close connection between the animal or bird and the plant on which it lives is obviously a potential danger to it. A severe drought, a fire, a flood, or some other natural cataclysm, such as is not uncommon in deserts, may exterminate bird and plant together, at any rate over a part of their range.

The plants which are most important as fodder for domestic animals in deserts belong to those perennials which live above ground at all seasons. Sheep in the more arid parts of Australia depend largely upon salt-loving succulents (Zygophyllaceæ and Salsolaceæ), particularly during periods of drought, and in the drier parts of the southern United States plants of the Cactus family are used in the same manner.

I can recall only one instance of animals dependent upon plants for water and not for food, and that was observed in the hill country of Palestine, which is certainly not desert, and barely falls within our definition of semi-desert. However, in the rainless summer, the season at which this observation was made, the country is extremely arid, and the observation is, I think, suggestive enough to warrant inclusion here. All over the hills of Judæa and Samaria there grows a genus of stout thistles (Echinops) with spiny globular heads. These flower in June and July when water is very scarce.

A large weevil (*Larinus maculatus*) and a Rose Chafer (*Protœtia libani*) bite into the flower-heads of this thistle, and feed on the interior, leaving an open wound from which the sap continues to run. This sap is drunk greedily by small bees, and wasps, and ants, and would not be available to them unless the weevil or chafer had first bitten into the thistle. Such a method of obtaining drink is not, of course, peculiar to desert climates; the sap which exudes from tree-trunks injured by Goat Moth or other wood-borers, in Great Britain, attracts butterflies, beetles, flies, and other insects.

Cases in which the animal depends on a plant for food and water might be multiplied. The relationship between Dwarf Gerbille and Suæda, in which protection as well as food and water is involved, leads us on to another group of associations, in which the principal or only bond between plant and animal is shelter from climate or protection from enemies.

Such an association was studied by Hartert in the northern Sahara, a short distance south of Biskra, in Algeria. He describes it thus: "After leaving Bordj Saada the tamarisk bushes disappear and a wide sandy plain covered with innumerable stones extends to far beyond Bordj Chegga, where the sand begins to prevail more and more. The sandy plain, however, is not smooth or even, but covered with countless little sandhills, the nucleus of which is, or has been in each case, a bush of *Limoniastrum*, *Salsola*, or other plant. Each isolated plant arrests the sand that flies across the

plain with every wind, and winds are frequent, and a miniature dune is formed; the plant is partly protected by the surrounding sand, but the latter runs down from the top and threatens to suffocate the plant, so that it strives for air and grows upwards, dying off at the lower end. Thus the hillock grows and grows and is crowned with a plant, until the latter dies off and a little mountain remains. These sandhills, hardened more and more in the course of time, form the centres of all the animal life except some of the birds. In these hillocks a rodent, *Meriones getulus,* the Djerd of the Arabs, makes its holes, which are used for nesting by *Œnanthe* (*Saxicola*) *mœsta,* and are sometimes inhabited by the dreaded, deadly Asp (*Cerastes cornutus*), the Lefa of the Arabs, and a beautiful, harmless snake, *Zamenis diadema.* In these hillocks one sees disappearing the pretty lizard, *Acanthodactylus scutellatus,* and in them hides the nocturnal Gecko, *Stenodactylus guttatus.* Also the beetles, the common *Anthia sexmaculata* and *Graphipterus,* and the rare and gigantic *Anthia venator,* as well as some Tenebrionidæ, disappear among these hillocks, the former with wonderful swiftness. In this sandy plain also, stony patches occur, like little islands in the sea of sand, and on these is found the pale Crested Lark (*Galerida theklæ deichleri*). Along the roads and on the sand we see another species of Crested Lark (*G. cristata arenicola*), which it is almost impossible to miss, while the first form is easily overlooked when one does not know exactly where to search for it; this was the reason why

Fig. 41.—Giant Cactus (*Cereus giganteus*), in which were found Nests of Gilded Flicker and Screech Owl: near Potholes, Colorado River, California. (*Photo:* Dr. J. Grinnell, Museum of Vertebrate Zoology, University of California.)

we only discovered its real home on our way back." Here the bond between the animal and the plant is mainly that the animal obtains shelter from the plant, or from the sand accumulated by the plant; but we know from other sources that the "Djerd," as well as other Gerbilles, are largely dependent on the Limoniastrum leaves for food and water.

A most interesting case of the same nature, but one in which the animals obtain shelter, but not food or drink, from the plant, has been studied in Arizona and California, by Grinnell and other American naturalists. The Saguaro, or Giant Cactus (*Cereus giganteus*), is a picturesque and very interesting inhabitant of those deserts (Fig. 41). It is an upright cylindrical plant, with very few branches, and covered with spines; it attains a height of 30 or 35 feet, and a diameter of 2 feet 6 inches. Its fruit is attractive to many species of birds, and according to Tuomey "nearly half a hundred birds feed upon the fruit of the Giant Cactus, the list including all our thrashers, woodpeckers, finches, and pigeons." But the Giant Cactus is not interesting only because birds eat its fruit, and as it harbours few insects one might suppose that there would be no close link between it and the birds for the great part of the year. A connection however exists, and it is a very close one. To quote from Grinnell: "It is clearly apparent that the critical feature of the saguaro which prescribes its avian dependants is nothing less than the favourable opportunity offered for the excavation of safe retreats in its trunk: and

only the two woodpeckers are equipped for making these excavations. So that, without the woodpeckers to make holes, the other birds would be no better off for the presence of saguaro." The two woodpeckers to which he refers are the Gila Woodpecker (*Centurus uropygialis*) and Mearn's Gilded Flicker (*Colaptes chrysoides mearnsi*). The range of these woodpeckers is wider than that of the Giant Cactus, and they have been found breeding in trees of various species along the banks of the California River. But wherever the Giant Cactus grows the two woodpeckers are found, and found more commonly than in other places, and when it is possible the woodpeckers hew their nesting-hole in this plant and nothing else. But for its existence the birds would be confined to the river-side growth of cottonwood and willow; but as they can excavate nesting-sites in the cactus they are able to colonize desert areas where no other large vegetation grows. Other parts of the same deserts where there is no Giant Cactus have a much poorer avifauna, for neither the woodpeckers nor the birds which are dependent upon them are found there. The association between the Giant Cactus and the two woodpeckers is closer because the woodpeckers are strictly resident birds, remaining all the year where they breed, and not wandering far from that place at any season. As Grinnell implies in the passage which I have quoted, other birds use the woodpeckers' nesting-holes, after the woodpeckers have vacated them. The Elf Owl (*Micropallas whitneyi*) is found exclusively in deserts

in which the Giant Cactus grows, and takes a disused woodpecker hole for its nesting-place. It is therefore dependent for its very existence on the presence of a particular cactus, and either of two particular woodpeckers. Less strictly dependent upon the cactus and woodpeckers are a Screech Owl (*Otus asio gilmani*), a Sparrow Hawk (*Falco sparverius*), a Flycatcher (*Myiarchus c. cinerascens*), and other birds. None of these are confined to the area inhabited by the Giant Cactus, but they all inhabit that area, and within it they all use old woodpecker holes as nesting-sites.

Frequently a single trunk of the Giant Cactus contains nests of one or other woodpecker, and also of one of the birds which use the old woodpecker holes. Honey-bees also use these excavations as hives. One must remember that the number of living creatures which eventually depend upon the Giant Cactus includes the scavengers in the birds' nests and bees' nests, the insects, few though they may be, which devour it or frequent its blossoms, and many others. All these organisms depend upon the growth of *Cereus giganteus* for their existence in certain areas.

There are instances in which, contrary to the general rule, the plants are dependent upon the animals, and although these cases are not very common in deserts, a few may be mentioned. Botanists tell us that there are two important agents, the wind and the insects, by which the pollen of plants is carried to the female flower, or female part of the flower, which it is intended to fertilize. In many

environments the insects fertilize more plants than the wind does ; in deserts, perhaps because winds are so common and blow without impediment among the sparse vegetation, fertilization by wind is much commoner than fertilization by insects : but the insects, especially the bees, flower-eating beetles, butterflies, and thrips, which are often so numerous among the annual vegetation, no doubt fertilize certain species of plant, though at present we have no clear knowledge on this point. One remarkable fact is known : *Loranthus acaciæ,* a plant related to the mistletoe, grows around the Dead Sea and in the Lower Jordan Valley, as a parasite upon various trees : it is almost certainly fertilized by the Sun-bird (*Cinnyris osea*), which probes the tubular blossoms with its long, curved beak.

According to Kobelt the Marmot (*Arctomys bobac*) of Mongolia materially alters the character of the vegetation round its colonies. The soil which is thrown up round the burrows is suitable to special plant types which are not common, and do not occur together elsewhere in the steppe : round the colonies of this rodent, and in no other place, these peculiar " marmot gardens " are found. Bateson states that in the very uniform steppes of Central Asia man and his animals are a disturbing factor. Old camp-sites can be seen from a great distance, because of the patches of nettles which grow on them and not in other parts of the desert.

The dispersion of seeds by birds and animals is common to all parts of the world. Seeds which are particularly suited to this means of conveyance are

generally provided with hooks with which they entangle themselves in the feathers or hair of passing creatures; others are produced in a fleshy pulp, which is eaten, and some at any rate of the seeds pass unharmed through the intestines of bird or mammal, or stick to its exterior until they are deposited perhaps at a distance from the parent plant. Numberless examples of seeds and seed-vessels armed with hooks and spines could be quoted from the flora of the Great Palæarctic Desert, especially from the annuals; it is a common thing to find such "burrs" in large numbers in the coats of sheep, jackals, and even such smooth-haired animals as gazelles and jerboas. Fleshy fruits are not common in deserts, and many of those which occur are so bitter or nauseating, or in other ways unattractive, that they are shunned by the fauna. Schimper states that jackals disperse the seeds of *Citrullus*, presumably after biting the fruit, but I do not think this is a common occurrence. The fruits of many members of the Cactus family are sweet and fleshy, though protected by spines. I have already quoted Tuomey's remarks about the fruit of *Cereus giganteus* and the birds which are attracted to it; Spalding adds that squirrels fatten on the fruit of *Echinocactus;* one is probably justified in concluding that the seeds of the Cactus family are largely spread by animals and birds. The date-palm (*Phœnix dactylifera*) is entitled to a place on the list, though palms which produce fruit edible to man do not exist wild.

Dates in Mesopotamia are eaten greedily by

several birds, but by none more than by *Hypocolius ampelinus.* These instances must not be supposed to imply that fleshy fruits are common in deserts; the reverse is the case.

Animals serve the plants by distributing their seeds, but they do immense harm to the vegetation by devouring plant and seed alike. The deserts of the Old World support large numbers of domestic goats, sheep, cattle, and camels, and of wild gazelles, antelopes, and hares, and these animals live by browsing shrubs and herbs. In the neighbourhood of a bedawin encampment or an Arab village or a frequented track it is almost impossible to find an untouched plant of any kind. Cannon observed in Algeria that the Mzabite cemeteries, in which the domestic animals are not allowed to graze, form a place of refuge to plants which otherwise do not exist at all near the haunts of man. It is frequently stated that thorns (page 62) are produced as a defence against these browsing animals, and this explanation may be true in some places, but certainly does not fit the facts very generally. In favour of the defensive theory is the fact that in the Southern United States and in parts of Australia, where species of Opuntia ("Prickly Pear") are used as food for sheep and cattle, only the thorny species can be successfully grown. If the thornless species are planted they must be protected by fencing against the grazing animals, and it is actually cheaper to grow the thorny species and to destroy the thorns by fire, when the plant is required for the stock, than to protect the thornless ones with fences. It is a fact

also, that certain plants which are without thorns spring up in the midst of a thorny bush of another species: in the Algerian Sahara the Terebinth or Betóum tree (Pistacia) is shielded by the Zizyphus, and in the Indian desert the Zizyphus protects the grass Andropogon in a similar manner. It is generally supposed that the Terebinth and Andropogon are protected from grazers by the Zizyphus, but one must remember that any plant which succeeds in establishing itself tends to shelter the soil around it, and to hold together the particles of soil if they are light and inclined to blow away. One well-established perennial plant mitigates the climatic conditions, and becomes the centre of a group of other plants of several species, and this will happen whether the perennial is thorny or not. It is possible, therefore, that the shelter which the Zizyphus affords from wind and heat is more important than the protection which it gives from grazing animals. Against the theory that thorns afford protection from grazing animals one may advance the fact already quoted that near human habitations, or frequented tracks, all desert vegetation, whether thorny or not, is stunted and deformed, or exterminated, because of the animals which graze upon it. From Central Australia we have Baldwin Spencer's evidence that the camel can eat every plant, from the spiny *Acacia farnesiana* to the juicy Claytonia. In the semi-deserts of Palestine camels prefer some of the more thorny shrubs, such as the Caper (Capparis), to others which are almost unarmed, but which are believed to be bitter, or nauseating by reason of taste or

smell; but Hart noted that they would eat Dæmia, a very milky Asclepiad. I have seen goats at Jericho climbing up to browse on Zizyphus twigs though the spring herbage was up to their bellies.

Furthermore, thorniness is most highly developed in the most arid deserts, exactly where large grazing animals are rarest, and the plants of the American deserts are on the whole more thorny than those of the Great Palæarctic Desert, though wild grazing animals are rare in the American deserts.

The majority of the cacti are covered with long, straight thorns, which mice use as if they were rungs on a ladder; the fruits (e.g. in Opuntia) carry small tufts of minute barbed hairs, which are easily detachable and very sharp; these are thickly set on the fruit, and it might be supposed that they would form an efficient defensive mechanism, but this is far from being the case. In the American deserts, in which these plants are native, the squirrels and mice eat the fruits in great quantity. In the Old World, where Opuntia is an introduced plant, the rodents have learnt to climb the plants and steal the seeds. At Jaffa two species of the genus are cultivated: the fruit of one is eaten by man; that of the other is opened by Gerbils (*Gerbillus allenbyi*), which gorge themselves and leave very few seeds to germinate. With the spiny fruit of Opuntia we may contrast the native and apparently defenceless gourd of *Citrullus colocynthus*, the Colocynth, which is not eaten by rodents or ruminants or jackals, apparently because it is bitter and violently purgative, and the Water Melon (*C. vulgaris*), which

is even more defenceless, for it is neither bitter nor purgative, and yet it frequently escapes from cultivation and thrives without protection from man in India, Palestine, and doubtless other places.

The conclusion to which these facts lead me is that thorns were not developed as a defence against grazing animals or rodents, and that they do not usually act in that way: I freely admit that they occasionally may exercise such a defensive function. They were probably developed in the first place as a response to the dry atmosphere.

CHAPTER VII

THE COLOURS OF DESERT ANIMALS

There is no doubt that the colour of desert animals is in some way the result of the conditions under which the creatures live, because it is quite characteristic of them, and not of animals from other types of country. Whether this colour is due to climate or is protective we do not know, and I propose first to discuss the facts and then to examine a theory that has been brought forward to explain them.

The majority of the animals which live in deserts are coloured buff, or sandy, or reddish-grey, and as plants are scanty and only very rarely cover the surface of the earth, we may say that generally the desert fauna resembles the ground on which it lives.

Furthermore, the colour of the typical desert creature is uniform, without remarkable pattern on the upper surface. A few birds, such as the Horned Lark (*Eremophila alpestris bilopha*) and the Cream-coloured Courser (*Cursorius gallicus*) and a few Gazelles among the mammals, have blackish markings on the head, but such a pattern is exceptional.

Though the dorsal surface of most desert animals appears to a careless glance to be of one colour,

when a specimen is examined closely it will often be found that the general unicolorous effect is produced by fine mottling. In the Palæarctic region we have many examples of this; among the birds the Egyptian Nightjar (*Caprimulgus ægyptius*), many Sandgrouse (Fig. 34), especially females, Hey's and See-See Partridges (Ammoperdix); among the mammals several foxes and gerbils, in which a general sandy tone is produced by the presence of black hairs or black-banded hairs among the pale hairs; many moths, especially Geometridæ, in which a unicolorous appearance is produced by fine and inconspicuous banding or mottling; in fact, fine vermiculation, producing a general impression of "self-colour," is common.

In many desert mammals the under-surface is very pale or quite white. It is a fact that desert species and sub-species differ from their near relatives from other environments just as much in their pale ventral surface as in their buff or sandy backs. Moreover, the pale ventral area is often more enlarged up the flanks of a desert mammal than it is in its relatives from other environments. This paleness of parts of the animal which cannot normally be seen extends even to the sole of the feet: Sumner states that "the soles of the feet of desert deer-mice are nearly or quite lacking in pigment, while those of mice from the more humid coastal regions vary from purplish to nearly black."

This type of coloration is found in all groups of animals which inhabit deserts; in spiders and centipedes and wood-lice; in moths, bugs, beetles,

bees, flies, grasshoppers, and wasps ; in many lizards, and snakes ; in many birds of many different families, larks, finches, warblers, owls, partridges, nightjars, waders, and others ; in many mammals of many groups, rodents and insectivores, and bats and ungulates and marsupials. In fact, I cannot quote a single group of animals which lives in the desert and which does not furnish examples of this general truth. The only apparent exceptions are to be found in certain groups of beetles and other small Arthropods which live their whole life below the surface of the ground.

This type of colour and of pattern which we have come to recognize as characteristic of the fauna of deserts is not only widely distributed in the animal kingdom, but widely spread over the world. In any desert, in any of the five continents, you will find these sandy or buff birds and mammals and insects, and you will not find them in numbers in any environment which is not desert or semi-desert.

Further, it may be stated that desert-dwelling animals are not coloured isabelline, or reddish buff, or greyish, indiscriminately ; for there is often a very close similarity in colour between the creature and the soil of the particular type of desert on which it lives. Thus, Lucas and Frost, in discussing the lizards collected by the Horn Expedition in Central Australia, refer to the "presumably protective coloration of the species of diurnal habits. Many of these exhibit a very marked general rustiness, or even bright redness, in their general colouring, which is quite wanting in the forms met with in the South

and East, and which agrees well with the colour of the red sands upon which they were captured." These authors also quote Prof. Spencer's field notes made on the same expedition, with regard to an Agamid lizard (*Amphibolurus barbatus*): "On open country to south of Charlotte waters, a general yellow-brown colour—similar to general colour of ground, with withered grass, etc.," which is contrasted with the series collected "at Crown Point, where plenty of red sand was, a peculiarly brick-red colour much resembling the colour of the sandy hills close to the camp where it was found." It is particularly interesting to find that this species so closely resembles two different types of desert soil, for it is widely distributed in Australia, and by no means specialized to a desert environment. The birds, too, furnish the most beautiful examples of species coloured so as to be well-nigh invisible among their native stones so long as they remain motionless. One of the Crested Larks (*Galerida theklæ*) is represented by a dark race (*G. t. harterti*) in the northern parts of Algeria, which are not desert; in the semi-deserts which fringe the Atlas Mountains southwards this is replaced by a paler race (*G. t. hilgerti*); in the Northern Sahara itself a still paler race is found (*G. t. deichleri*), which "is so wonderfully adapted to the soil that it is easily overlooked if the birds do not happen to be on the wing or singing" (Hartert). Between Laghwat and Ghardaia a reddish form (*G. t. carolinæ*) of this species is found, and its distribution corresponds fairly closely with the reddish stony desert. The

colour and distribution of these races finds its parallel in the hares, *Lepus pallidior*, which is pale and greyish and is found along the south side of the Atlas Mountains, and *L. whitakeri*, which is reddish sandy, and is found in the country round Ghardaia. Meinertzhagen has studied certain races of another species of Crested Lark (*Galerida cristata*) and arranges them thus, beginning with the darkest and ending with the palest.

Race.	Soil.	Locality.
Nigricans . .	Black alluvial	Central Egyptian Delta
Maculata . .	Dark alluvial with a percentage of sand	Cairo, Helwan
Meridionalis .	Dark brown, often red	Crete
	Dark brown	*Cyprus*
Cinnamomina	Reddish	Beirut
	Brown	Haifa
Zion . . .	Brown to pale brown	Damascus, Tiberias, Jerusalem
Brachyura .	Pale brown and sand	Suez, Gaza, Sollum, etc.

He quotes also the mean relative humidity and the mean rainfall of the localities, both for the year, and for the months April and May, when the birds are breeding. He concludes that "Crested larks are influenced in the colour of their plumage by protective resemblance to the soil on which they live, and that neither humidity nor rainfall has any effect on their plumage. This same influence seems to affect nearly all ground-birds which more or less live in the open, such as *Ammomanes*, *Alæmon*, *Œnanthe deserti*, *Eremophila*, *Alectoris*, *Pterocles*, etc."

For reasons which I shall give later I am not convinced that the resemblance of birds to soil is "protective," if by that word it is implied that the resemblance affords protection from enemies, but let us accept it that there is a close similarity between the colour of the bird and the colour of its native soil.

It is also interesting that in the first plumage these Crested Larks show very much the same differences in shade as do the adults of the same sub-species. The feathered young of *G. c. brachyura* is, for instance, paler than that of *G. c. nigricans*, and both of them are very much paler than specimens of *G. c. cristata*, the Central European race.

A somewhat similar case is that of the Houbara Bustard. The typical sub-species (*Chlamydotis u. undulata*) inhabits the Sahara and Southern Morocco, and is of a mottled sandy colour, which accords well with the pale and sandy soil on which it lives. In the Eastern Canary Islands (Fuerteventura and Lanzarote) the sub-species *C. u. fuerteventuræ* is found: it differs from the typical sub-species in the speckling and mottling of its upper surface with black; it harmonizes very closely with the lava-strewn wastes of these islands, and the typical pale race would be extremely conspicuous upon them. Accurate information with regard to the humidity of the air and the rainfall of these islands is lacking, but Bannerman attributes the blackening of the island race to its existence upon the blackish lava.

It seems to be agreed among American zoologists

that mice, wood-rats, and other small mammals which inhabit areas of blackish lava as well as other parts of the desert are often darker on the lava than elsewhere. It is fair to mention that this has recently been controverted by Sumner, who has shown that in some cases, at any rate, the darker colour may be due not to living on lava, but to differences in other environmental factors, such as rainfall. In the case of one animal (the deer-mouse, *Peromyscus crinitus*), he was able to show that if long series of this mouse living on black lava and on "pale grey, buff, and pinkish" rock were compared, no difference in tone could be detected either by eye or by photometer.

Other cases occur in which the resemblance of animals which are, broadly speaking, "desert-coloured" to their particular type of desert, is by no means very close. I remember obtaining four species of mammalia at Qazvin in North-West Persia: the local fox was greyish sandy with a reddish saddle; the hare was pinkish buff; the gerbil (*Meriones blackleri lycaon*) was yellowish buff; and the dwarf hamster (*Cricetulus*) pure pale grey without any trace of yellow or buff colour. All these occurred on the same ground, and any one of them was a good example of "desert coloration," but none of them resembled the exact shade of the soil at all closely.

In Mesopotamia downy young of the Sandgrouse *Pterocles senegallus* and *P. exustus* have been obtained in the same type of pebble and clay desert, but they differ widely both in pattern and colour.

Grinnell has recorded a similar phenomenon. Speaking of "conies" (*Ochotona*), by which an animal very different from the biblical cony or hyrax is meant, he says, "as elsewhere, the conies in the white mountains live in rock slides and broken-up rock out-crops." Two colours of rock occur in this range, a blackish or dark red 'shale,' and a white or greyish white granite. There are extensive belts purely of one or the other kind of rock. Our party took pains to shoot conies from each colour of ground, keeping notebook record of where each specimen was shot. I am unable to detect any difference in colour between animals shot from white granite and those from dark 'shale.'"

Speaking of the Roadrunner (*Geococcyx californianus*), a large, ground-loving Cuckoo found in California, he remarks that "it is, of course, a remarkable exception if the Roadrunner, a terrestrial, permanently resident bird of all the areas it inhabits, should not show some geographic colour peculiarities. Indeed, it is all the more strange that it does not show conspicuous differences in colour tone in the arid and subhumid areas it occupies, when we observe the remarkably different colour tones exhibited by the thrashers, towhees, spermophiles and jack rabbits of the same areas, these also being terrestrial animals. The Roadrunner's failure to conform to the rule offers a problem for those who would explain animal coloration wholly on the ground of physiological response to meteorological conditions, irrespective of adaptive value."

Certain desert insects attain a silvery or sandy

appearance by being clothed with hairs of that colour; many of these insects settle rarely or never on the desert soil, so that their case deserves special consideration. The phenomenon is found in many bees, wasps, and fossors, and in at least three families of flies (Bombyliidæ, Nemestrinidæ, and Tabanidæ). That is to say that it has been evolved on a number of separate occasions to suit the particular needs of insects that fly or hover over deserts. Morice was, I believe, the first to call attention to it in Hymenoptera, remarking that "no one, I should think, who has collected in the deserts of Algeria, Egypt or Palestine can doubt that the very pale colours and shimmering silvery or golden pruinosity, so common in all groups of Hymenoptera in such localities, and practically there only, are cryptic characters, rendering the insects which possess them inconspicuous and almost invisible among the glittering sand and pale vegetation which they haunt. Here at least, contrary to the rule laid down by Wallace, we have stinging Hymenoptera coloured so as to resemble, or at any rate so as not to contrast with, the inanimate and vegetable substances which normally surround them." I have quoted *his words* because they describe the facts excellently; his suggestion that the colours are "cryptic" is a topic to which we shall return later. A similar condition prevails in the gad-flies (Tabanidæ), many species of which from Mesopotamia and South Palestine are clothed with down of a pale tawny colour. This is remarkable, because the gad-flies rarely settle on the ground or on rocks except

at night, and spend most of the daylight hours visiting flowers or sucking the blood of the larger animals. Certain flies of the families Bombyliidæ and Nemestrinidæ exhibit the same type of coloration, though they spend their time at flowers or hovering in the air: they do not rest on the soil which they so closely resemble in colour.

We find, then, that most of the animals which live in deserts are coloured buff or sandy or pale grey; bold pattern is rare; this type of colour is exhibited by animals of nearly every group, and is prevalent in the deserts of every continent. It is even characteristic of some insects, not closely related to one another, which spend the hours of daylight in the air or on flowers and not on the surface of the desert. As to the effect of these colours upon the human eye it must be acknowledged that the prevalent buff and sandy colours of desert animals do render them extremely difficult to detect, unless they move. This is probably as much due to their immobility as to their colour. Every naturalist who has ever visited the desert has noticed this, and it is true of all the manifold forms of life which exhibit these colours. The most remarkable example that ever came to my notice was in Baghdad, Mesopotamia, in September. There was a small patch of ground of perhaps an acre, walled off but not at that season cultivated. In it one could always be certain of finding at least a score of Egyptian Nightjars (*Caprimulgus ægyptius*), but though the ground was absolutely bare, and though I visited the place repeatedly, I never succeeded in detecting

a Nightjar before it flew, and this in spite of the comparatively large size of the bird. We must admit it as a fact that the prevalent colour of desert animals does render them most difficult to see so long as they remain motionless.

There is only one important exception to the generalization that desert animals resemble in colour the soil on which they live, but it is a most remarkable one; in many deserts a number of the indigenous animals are black. This is not commonly known, but is none the less fact. Speaking generally, it may be said that any desert creature which is not coloured like its surroundings is black, for bright greens and blues and reds and yellows are very rare; and though black animals are not a dominating element in the fauna, they are sufficiently numerous to be noticeable in many places in the Great Palæarctic Desert. The most remarkable group of black inhabitants of deserts are the Tenebrionidæ, a family of beetles. Members of this family, to which the meal-worm (Tenebrio) and the Cellar Beetle (Blaps) belong, are found in a great variety of environments in nearly all parts of the world. The majority of them are black, and nocturnal; the habits and food of these insects are very imperfectly known, but it is believed that the larvæ and adults of most feed on dried vegetable matter, and refuse generally; possibly their ability to live on dry food has enabled them to invade the arid areas of the globe. Whatever be the reason, the Tenebrionidæ have proved successful in colonizing arid countries, and, as the following list shows, all

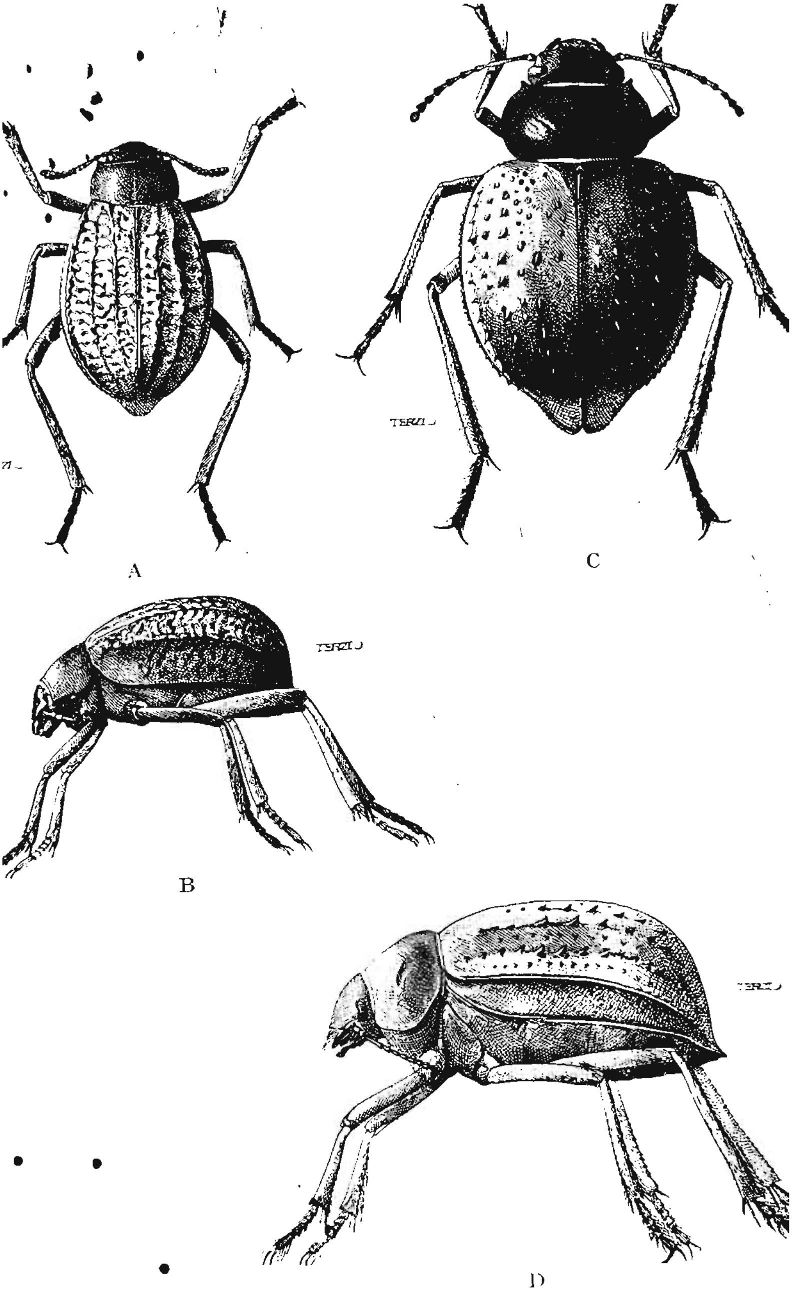


Fig. 42.—Typical Black Diurnal Tenebrionid Beetles of the Great Palæ-tic Desert (× $4\frac{1}{2}$). A. and B, *Adesmia ulcerosa*; C and D, *Pim angulata*. (E. Terzi.)

the large deserts of the world are inhabited by one or more of the many sub-families into which these insects are divided :—

Sub-family.	Desert inhabited.
Erodiinæ	Palæarctic
Zophosinæ	,, and African
Tentyriinæ	,, ,, ,,
Adesmiinæ	,, ,, ,,
Eurychorinæ	South African
Cryptochilinæ	,, ,,
Molurinæ	,, ,,
Sepidinæ	Palæarctic and African
Akidinæ	,, ,, ,,
Pimeliinæ	,, ,, ,,
Blaptinæ	,, ,, ,,
Eleodinæ	American
Praocinæ	,,
Coniontinæ	,,
Adaliinæ	Australian
	(K. G. Blair in litt.)

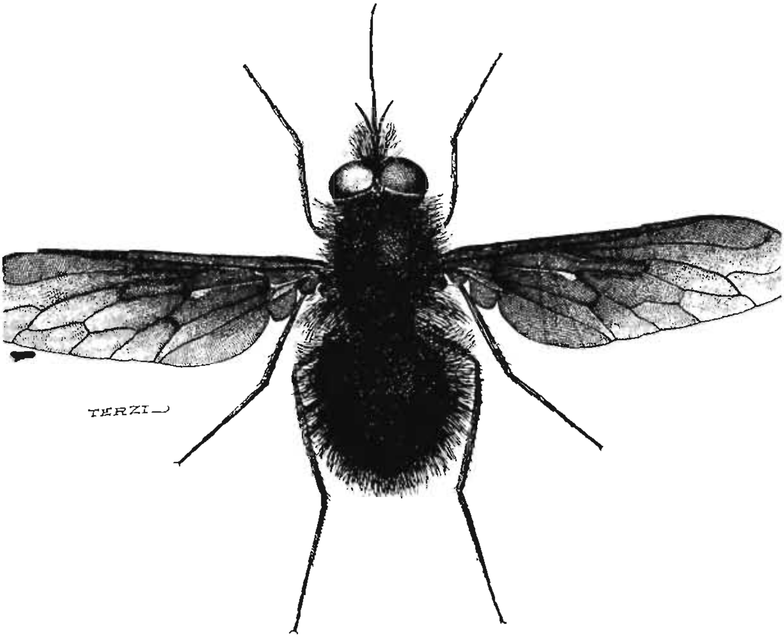
Blackness, as I have said, is characteristic of the Tenebrionidæ. The desert environment has not affected them, for in all the deserts in which they occur the majority of species remain black. As many of them are nocturnal, and as they shelter by day under rocks, this is not at first sight remarkable, but it is very remarkable that others have acquired a habit of wandering over the naked ground by day, and that these retain their uncompromising black colour. Examples familiar to the traveller in any of the deserts of Algeria, Egypt, Palestine or Persia are the genera Adesmia and Pimelia (Fig. 42). These are large black active insects, and they are a dominant part of the fauna of these countries in winter, spring and early summer. Their activity is strictly diurnal, for they do not take refuge from

the midday sun, but retreat under stones at night, and during cold weather.[1] As these insects are so numerous and so visible one naturally wonders how they protect themselves from insect-eating birds and lizards. It appears probable that they are to some extent saved from destruction by their size and their hardness : this is an inadequate protection, for the late G. Storey shot a young black and white Wheatear (species ?) in Wadi Hof, near Cairo, and found that it was stuffed with Adesmia, and Radde recorded long ago that the Red-footed Falcon (*Falco vespertinus*) eats Blaps and Pimelia on the Simferopol Steppes in April.

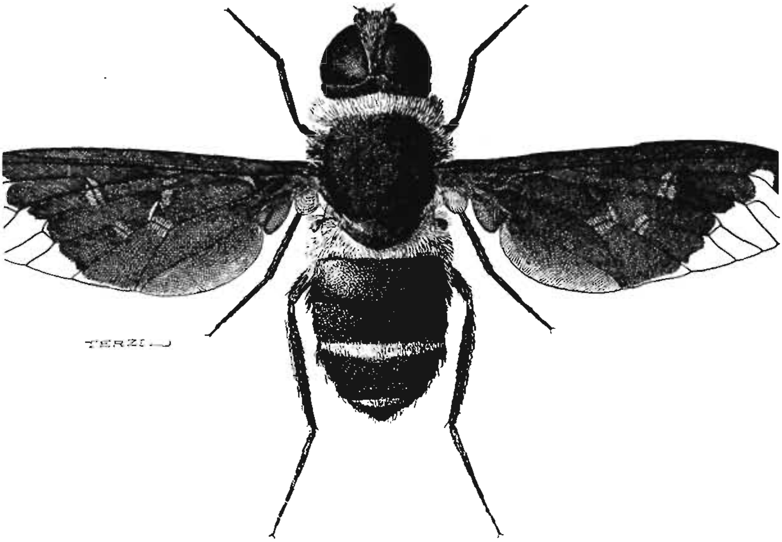
The anomaly of the black colour and diurnal habits of these insects is heightened by the fact that some desert Tenebrionidæ are dull brown, others are black and hairy, but they cover themselves with an earthy or dusty coating which is difficult to remove ; these inconspicuous Tenebrionidæ are nocturnal insects, and it is difficult to see that their camouflage is of value to them.

Black members of the Chafer family of Beetles, among them the familiar " Scarab " of Egypt and other countries along the Mediterranean littoral, occur in many places in the Great Palæarctic Desert, but they are neither so common nor so characteristic as the Tenebrionidæ. Among the flies there are several species of Bombyliidæ in the Great Palæarctic Desert, which are black, or predominantly black. Fig. 43 shows a member of (*a*) the Bom-

[1] This statement is probably true of all species of Adesmia and of many Pimeliæ (e.g. *P. angulata*, Fig. 42): other members of the genus are nocturnal.



A



B

43.—Typical Black Diurnal Flies, from Palestine, belonging to diffei ent sub-families of the Bombyliidæ (× $4\frac{1}{2}$). A, *Bombylius fuscus* (Bon byl̇inæ) ; B, *Hemipenthes* sp. (near *H. velutina*), (Anthracinæ). (E. Terzi

byliinæ, and (*b*) the Anthracinæ, a sub-family in which this phenomenon is quite common.

In the Algerian Sahara among the numbers of active black Adesmia one may frequently capture a large Long-horned Grasshopper, black and shiny, with red processes on the thorax. This insect is *Eugaster guyoni*. In contrast to the active Adesmias, it is a very sluggish insect and its hindlegs are not specially lengthened and strengthened for jumping as they are in nearly all its relatives. Further, we may suppose that Adesmia and the other diurnal Tenebrionidæ are black by inheritance, and that they have retained the family's colours not because it was directly advantageous, but because it was not disadvantageous. No such reasoning can be applied to Eugaster, which belongs to a family in which shiny blackness is extremely rare : we are therefore left to wonder at its assumption of this colour and at its abrogation of the power to jump. Eugaster is extremely conspicuous and deliberate in its motions ; when it is handled it pours forth a copious brown oily secretion, and it is tempting to suppose that this protects it from insect-eaters ; we have absolutely no evidence that this is the case.

Among the Short-horned Grasshoppers (Locustidæ or Acridiidæ) there is an interesting species, *Calliptamus cœlesyriensis*, which ranges from Palestine to Turkestan. In Palestine it occurs in semi-desert country among withered annual vegetation in the months of May and June. One common form is very dark chocolate brown all over, except that the ventral surface is slightly paler. I have nearly

always found it associated with much greater numbers of a pale buff form of the same species; intermediates between this and the chocolate form do not occur in my experience. It is remarkable that two varieties of one species, living in identical environmental conditions at the same season of the year, should be so differently coloured, the common form resembling the surrounding stones and dead herbage in colour, as do nearly all other members of the family, the rarer form being nearly black and very conspicuous. Another member of the same family (*Pœcilocerus bufonis*) in Sinai is dimorphic in a similar manner.

In most parts of the Great Palæarctic Desert, birds which are mainly or entirely black are found. Excellent examples are afforded by the Ravens and by a large number of species of black and white Wheatears and Chats (Saxicola). The latter range right across the Great Palæarctic Desert, from Rio de Oro and Morocco to Turkestan, Sind and Rajputana. Inside the belt of desert and semi-desert they are abundant both as species or as individuals, and outside it they are rarer, and occur for the most part as stragglers. Blackness is not an ancestral colour for Wheatears and Chats, and is quite exceptional among them. One can trace a progressive series among the desert members of the genus, showing the gradual replacement of buff by white, and then the replacement of the white by black.

In some species the blackening has proceeded further in the male than in the female, in other species both sexes are equally black. It appears

therefore that these birds have evolved their blackness because in some way it fits them to a desert existence; in this respect they resemble *Eugaster guyoni* and the dark form of *Calliptamus cœlesyriensis.* This is the more remarkable because within the limits of the same genus (Saxicola) there are birds which inhabit the same deserts and which are coloured like the soil on which they live; examples are the Isabelline Wheatear (*S. isabellina*) and the Desert Wheatear (*S. deserti*), both of which are widely distributed in the Great Palæarctic Desert, and occur side by side with various black and white congeners. The habits of the black and white Wheatears closely resemble those of the other members of the genus, that is to say that they are wary birds, given to perching on upstanding rocks and, at any rate to my eyes, easy to see when they are sitting still, and extremely conspicuous when they move.

Among the reptiles there is one species which becomes increasingly black beneath as its habitat becomes more and more strongly desert. Hartert has recorded that the spiny-tailed lizard (*Uromastix acanthinurus*) of Biskra, El Kantara, and other places in the northern part of the Algerian Sahara is replaced farther south in the Mzab country by a form which is much blacker on its ventral surface, and that this in turn is replaced in Tademait and the central Sahara by a form in which the males are quite black, and the females nearly so, all over the under surface of the body and the tail. This very remarkable case can scarcely be grouped with those which

we have already considered as the increased blackness of the more desert forms of this species is confined to the invisible ventral surface.[1]

I can find few records of the occurrence of black diurnal animals in any desert outside the Palæarctic region: it is possible that black animals occur and that no one has called our attention to them. It is interesting to notice that Merriam refers to the Tenebrionid genera Eleodes and Asima as common and characteristic in the Painted Desert, in America. Hudson speaks of *Galictis barbara*, a "quaint-looking weasel, intensely black in colour, and grey on the back and flat crown"; this animal is diurnal and hunts in companies on the pampas of La Plata. In the same country is found *Didelphys azaræ*, a black and white oppossum: this animal is also diurnal. It is, of course, possible to suppose that these two totally unrelated conspicuous diurnal predatory animals exhibit "warning coloration," a topic too large to be considered here.

I have summarized the facts; let us now see whether they are capable of explanation. Many of us, during our childhood, were taken to the Natural

[1] Among the Amphibia and Reptiles which inhabit deserts there are species which develop brilliant colours in the wet season in such a way that they become extremely conspicuous. This brilliance reaches its climax after pairing has taken place, and is common to both sexes of the frog or lizard concerned. For details consult C. L. Camp, *Notes on the Local Distribution and Habits of the Amphibians and Reptiles of South-Eastern California in the Vicinity of the Turtle Mountains*, Univ. of California Publications in Zoology, XII, p. 511 (Aug. 12, 1916), and Baldwin Spencer, *Report on the Work of the Horn Scientific Expedition to Central Australia*, Part I, pp. 26, 27 (1896).

History Museum in Kensington, and shown the large case which illustrates desert life. We remember the sandy rocks, the sparse dry vegetation and the birds, beasts and reptiles all coloured so that they were inconspicuous. We did not realize that they were inconspicuous, at any rate in part, because they were motionless, and that about half the creatures in the case were strictly nocturnal. We were told that the animals were so coloured as a protection from their enemies, and most of us have grown up without ever critically examining this statement, so that the theory of protective coloration is still widely accepted by people who are not strictly scientists, but are very deeply interested in biological problems ; the time has come to examine it very closely. This theory presumes that there are predaceous creatures from which the animal must be protected, or else that the animal is itself predaceous and that its colour enables it to stalk its prey with success ; the theory presumes also that the protection given is actually effective under natural conditions in the open desert. One asks at once from what enemies the desert creature needs to be protected. Admit that the moths, grasshoppers, mantids, spiders, and other small organisms are preyed upon by insectivorous birds and reptiles, and suppose that the colour of these small animals gives them some measure of safety ; the supposition is not based on accurate knowledge, but it is not unreasonable. Now, what are the enemies of the larger "protectively coloured" birds, the Sandgrouse (Pterocles) and Courser (Cursorius) ?

Falconers say that as a general rule trained Peregrines and Shahins cannot capture these birds except by chance, and that the ordinary desert Falcons, the Sakers and Laggers, are less swift than the Peregrines. It would seem, then, that the Coursers and Sandgrouse are protected from Falcons more by speed than colour. I know of no other predaceous animals which hunt by day and which may be supposed to chase Sandgrouse or Courser.

The real enemies of these birds are probably cats and foxes and possibly jackals; these all hunt by night and by scent, so that the colour of the bird motionless in a dim light can hardly have a protective value to it.

Now, let us consider the predaceous birds and animals—first those of diurnal and then those of nocturnal habits. The supporter of protective coloration supposes that they are coloured like the desert in order that they may more successfully stalk and seize their prey, that is to say that their colour *effaces* them. This ingenious explanation fails to cover the facts. The Merlin is fairly familiar to many of us as a small hawk, widely distributed in Europe and Northern Asia. It feeds largely on small birds and hunts on the wing; any colour and pattern which is to prevent the small birds from seeing it should therefore be on the under side of the bird. As a matter of fact, the ordinary western form of Merlin (*Falco columbarius regulus*), which does not breed in deserts, winters, among other places, in the deserts of Algeria, Tunisia and Egypt. Farther East, however, there is a race (*Falco columbarius*

pallidus) which breeds in the deserts and steppes of Central Asia ; this race is desert-coloured, being a very pale and delicate blue-grey above, and paler beneath than the western race. The western Merlin, which is not desert-coloured, is well able to find a living in the deserts in which it winters ; on the supposition that the Merlin requires effacing coloration, why is it necessary for the eastern race to be coloured very pale, and particularly why should the colour of its upper surface be paler than that of the western race ? A good parallel is afforded by the larger falcons. The Peregrine (*Falco peregrinus*), which is not a desert-breeder and is dark iron-grey above, winters in many of the Great Palæarctic deserts ; in these regions one finds also the Saker Falcon (*Falco cherrug*) and the Lanner Falcon (*F. biarmicus*), which are pale desert-breeders. One cannot see that the desert species have any advantage over the Peregrine during the months during which they live side by side.

With the Falcons the theory of protective coloration, or rather of effecting coloration, fails to cover the facts, but the effacing colour of other predaceous animals does help them to catch their prey. In the Californian deserts near the Turtle Mountains there exists, according to Camp, a Rattlesnake (*Crotalus cerastes*) which is coloured so that when it lies buried in sand flush with the surface it is well-nigh invisible. Invisibility, or some close approach to it, really is attained, and the snake and the lizards which form its prey are active by daylight at a time when the value of colour as an effacer must

be at its highest. Instances such as this are few, and the theory of protective or effacing coloration which explains them well enough cannot be extended generally.

In the case of nocturnal beasts and birds of prey it is still more difficult to explain colour as an effacer, because even by moonlight colour hardly exists, and differences between shades of colour are not appreciated. All the same, there is a large group of desert-coloured, nocturnal, predaceous forms, some like the owls hunting by sight, others like cats and jackals and foxes by scent. All are pale in colour, and from numerous examples, occurring in all deserts, I choose the following. Thomas has recently described a Caracal from Asben in the South Central Sahara. It differs from all known Caracals in its "exceptionally pallid coloration and silvery ears." It is "a desert-coloured form with whitish ear-pencils." Among the birds the Eagle Owl (*Bubo bubo*) is a wide-ranging species able to support itself equally in the forests of Scandinavia and the steppes and deserts of Persia, Transcaspia and Egypt. A large number of sub-species have been described and they form a most interesting gradation from the large dark forest birds of Europe and North-West Asia to such small and pale desert forms as *Bubo b. aharonii* in Southern Palestine; *B. b. ascalaphus* in North Africa and Egypt; *B. b. turkomanus* in Transcaspia, East Persia and Turkestan, and other forms.

There is, of course, a still larger group of animals which are preyed upon and which are nocturnal. Nearly all the Jerboas and Gerbils of the Old World.

and their counterparts in the American deserts and Australia (pages 74–80), are strictly nocturnal, and one may well question whether their beautiful sandy tints have much protective value. By moonlight, to the human eye they appear nearly white and rather conspicuous. Most of them, it should be remembered, are very strictly nocturnal: Jerboas (*Jaculus*) and Dwarf Gerbils (*Dipodillus*) may occasionally be seen when the daylight has nearly gone, but many other forms never come above ground until night has definitely fallen. In the summer and autumn of 1919 I was camped for four months outside Qazvin in the semi-desert of North-West Persia. All around us were the burrows of the Gerbils (*Meriones blackleri lycaon* and *M. erythrurus*), but never once did I see either of these animals by daylight, either in the dawn or after sunset: every night I was in the desert between 8 and 9 p.m., and I always saw Gerbils crossing the beam of my lamp. Without a lamp I found it impossible to see them except when the moon was bright, and then they appeared white and conspicuous. Devout supporters of the theory of protective coloration claim that animals, both predators and prey, are rendered inconspicuous even at night, perhaps by moonlight, by their pale colour; the claim seems to me to be more ingenious than probable, but I cannot disprove it. The whole question of visibility at night, with or without moon, is beset with difficulties, because we have only the vaguest knowledge of the extent to which habitually nocturnal animals rely upon their eyes in obtaining their food.

The difficulty of accepting the view that pale sandy tints "protect" the nocturnal animals of deserts is as nothing compared with the difficulty of accepting the same view with regard to certain subterranean forms. The Pocket-Gophers (Thomomys) of the southern United States are found in a variety of environments, including the deserts. They very rarely come above ground, but none the less those that live below the surface of the desert are paler than the others; the palest of all is *Thomomys albatus* described by Grinnell from the Imperial region of California. This form is actually the palest of all the animals of its native region; and all the mammals of the Imperial region, which is desert but not of an extreme sort, are very pale. It is interesting to learn that the soil in which this Pocket-Gopher burrows is by no means very dry.

The Marsupial Mole (*Notoryctes*), which is a purely subterranean inhabitant of sandy places in Central Australia, is pale sandy, frequently almost white, in colour. It is even more rarely exposed to daylight and to enemies on the surface of the soil than the Pocket-Gopher, and unless we postulate that both are descended from ancestors which lived on the surface of deserts and there acquired a "protective coloration," we cannot in any way account for their colour: for such an hypothesis there is not a shadow of evidence.

Similar examples occur among the Reptilia. The Sand Boa (*Eryx jaculus*) and the nearly limbless Skink (*Eumeces scutatus*) are animals which live

nearly all their lives underground : they are certainly paler and less distinctly marked when they live in the soil of deserts than when they live in the soil of wooded country, as my friend Capt. C. M. Ingoldby informs me.

It is generally true that bats of desert areas are paler above and below than their relations living in areas which are not desert. Many examples might be chosen from Persia, Mesopotamia, Egypt, and the American deserts to show that this difference is the rule. This very general truth hardly admits of an explanation as an example of "protective coloration," for predaceous enemies of bats must be rare ; and in any case they do not pursue the bat against a background of desert soil. The most likely enemies are owls, but in the Great Palæarctic Desert owls are on the whole not common, except the Little Owl (*Athene noctua* subspp.), which hunts in the dusk rather than at night and is not a serious enemy of the bats. From what enemy, then, are the bats "protected," and if a predaceous enemy exists does their protection not lie rather in their speed and agility than in their colour ?

I have endeavoured to show that the theory of protective coloration breaks down when we consider particular animals with reference to their prey or their predatory enemies. There are other instances in which the animal's colour should apparently give perfect protection were it not that its habits are unsuitable.

One must realize that colour assimilating perfectly to the natural environment will give little protection

unless the animal remains still. Abel Chapman has gone so far as to state it as an axiom that "absolute immobility, on the part of the object itself, is essential; to put it in other words that the slightest movement, even of a part, is fatal to the value of any protective principle." I think few of us would agree to so extreme a statement, but every field naturalist knows that it is movement which catches the eye more readily than colour, or pattern or even symmetry. The Cream Coloured Courser (*Cursorius gallicus*) is as perfect an example as one could find of a bird which is invisible in desert, so long as it is still; sometimes it crouches and then it defies detection in stony desert at 20 yards. More often it does not crouch when you approach it, but gets on its long legs and runs rapidly away; it stands high above the ground, casting a conspicuous black shadow in the bright sunlight, and trusts to its legs and not to its colour to ensure its safety. Even when it is not disturbed the Courser is very conspicuous when feeding in the early morning and late evening: as the sun is low it casts a particularly large shadow, so that at these times the bird is easy to see. The same may be said of many other desert birds which are beautifully "protected" if you see them in a museum, but are quite conspicuous in nature because they do not keep still. Most of the larks of the Great Palæarctic Desert (Ammomanes, Galerida and others) are rather foolish little birds which scratch and feed and chirrup within 20 yards of you, and you can only feel that a little ordinary intelligence would render them invisible. Hey's Partridge (*Am-*

moperdix heyi) and the See See (*A. griseogularis*) are two small Partridges with exquisite soft buff and greyish sandy feathers. All through the middle of the day they lie up in holes in rocks and under boulders: at the time they are, of course, invisible owing to their position, not their colour. When the sun is low they come out to feed; though their legs are short their shadow is long at this time of day, and they are quite conspicuous.

In certain grasshoppers it seems probable that the coloration is actually protective. Vosseler mentions the Short-horned Grasshoppers Eremobia, Eremocharis, Pamphagus and others, in all of which the thorax and abdomen are widened and flattened in such a way that the animal is triangular in transverse section and flat below. When it presses its ventral surface to the ground there is no shadow to betray it, and while at rest it carries the broad flat femora pressed against the abdomen, thus contributing to the same result. In this attitude every visible part of the insect is "desert colour," and is roughened so that it resembles rough rock or sand: bright colours occur on the hind-wings, on the inner face of the femora, and on intersegmental membranes, but they cannot be seen while the insect is at rest. It seems, then, that in these grasshoppers shape, colour, surface sculpturing and habit co-operate to render the insect difficult to see, and one must admit that in these cases the colour is protective, for it is unreasonable to argue that the shape, sculpturing and habit are protective, and that the colour with which they co-operate is due to

some other cause. Such cases as this are rare, and I maintain that the theory of protective coloration does not cover more than a few of the phenomena. For instance, among the invertebrata one may find examples of colour which would conceal an animal were its habits not faulty. The hovering flies and bees and wasps to which reference has already been made (page 148) are a case in point; so are many grasshoppers which climb on a stone and rub their legs together to make a noise, thereby betraying their position by their noise and movement.

I think, then, that we are justified in saying that many creatures whose colours would afford them complete protection if they kept still are rendered easy to see because their movements annul this protection: if the colour has a "protective function," then the habit has an "advertising function": a theory of advertisement might be launched, and could be almost as well supported as the more popular theory of protection.

And then how many colours there are which we must frankly say are unsuitable, unless we discard the theory of protective coloration. I have dealt at some length with the black forms earlier in this chapter: let us now consider them from the point of view of theory. Enthusiastic supporters of "protective coloration" have realized that a black and white Wheatear perched on a rock might raise doubts as to the soundness of that theory, and they have urged that these birds are not really conspicuous in a bright sun, among dazzling high lights and

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black shadows, so long as they remain still; unfortunately Wheatears are active, restless birds and do not remain still for long. If we grant, what no one who knows these birds in their haunts will deny, that they are very easily seen, we may suppose that they are protected from diurnal birds of prey by their extreme wariness. This might abolish the need for protective coloration, but does not in the least explain the assumption of black, or black and white colour.

Remember, also, that the black, or black and white Wheatears exist side by side with buff and isabelline congeners, and the nearly black race of *Calliptamus cœlesyriensis*, so far as we know, never replaces the normal buff typical race of its own species. The buff and black exist side by side and appear to fill identical places in the general economy of nature.

It is this recurrence of blackness, in widely separated groups of animals, which is so remarkable. If we may postulate that the Raven has no predaceous enemies, that Eugaster (page 153) is protected by its oily secretion from whatever enemies it has, and that the Wheatears evade the hawk by quickness and watchfulness, then we can understand that desert-colour is not necessary to these animals. But at once we are faced with their unanimous choice of black: if they are freed from the necessity of being buff, why are none of them green, or red, or blue? We must remember that black absorbs more radiant heat than any other colour. Presumably therefore a black creature must

evaporate more water than a similar buff creature, if it is to keep its body temperature below a certain figure on a particular day. This, one would suppose, would severely handicap the black creatures under circumstances in which water is extremely scarce.

And then, again, why in particular do Eugaster and *Calliptamus cœlesyriensis* and the Wheatears become black, for it is against their family traditions? The Raven and Tenebrionids and the Scarab, we may suppose, are black because the colour is ancestral and they found no reason to alter it; but the Eugaster and Calliptamus and Wheatears have broken with all tradition, and at present we cannot explain their blackness.

I maintain, then, that protective coloration cannot be accepted as a theory to explain the very remarkable coloration of desert animals. It is not easy to apply it to animals which hunt or are hunted at night; or to animals which appear to be without any large enemies more powerful than themselves, or to animals whose pallid colour extends to their bellies and the soles of their feet. It cannot be applied at all to subterranean animals, nor to black animals, nor to those whose colour would protect them if their habits were radically altered. I do not deny that protection is afforded by colour, under certain circumstances, to certain animals: on the contrary I readily admit that many desert animals are rendered invisible by their colour, which harmonizes perfectly with their particular environment: most of these animals are invertebrates and not rapid in

their movements: to these forms the theory of protective coloration may rightly be applied. The point upon which I wish to insist is that the theory only covers a small portion of the facts; we must look for some other cause, and suppose that after the prevalent buff or sandy colours had become established, certain of the creatures used them as a protection from their enemies: this is equivalent to saying that the protection afforded is quite a secondary matter and in no way causal.

If we are compelled to disavow our faith in protective coloration as the cause of this remarkable general depigmentation, to what are we to turn for an explanation? The cause is one which affects animals of every type, in every desert; it does not discriminate between prey and captor, between the creeping and flying animals, between the diurnal, the nocturnal, and the subterranean. It is so universal in its application that it is probably physical. No biological agency, such as the struggle with rivals for food or water, the avoiding of enemies, or seeking a mate, can cover so wide a range of animals; heat alone it is not, for heat in other parts of the world does not produce these uniform pale forms; low or fluctuating relative humidity it can hardly be, for the animals which live below stones and in burrows by day, and emerge at night, are not exposed either to very low or very fluctuating humidity. I am unable to suggest any condition, or combination of conditions, which can make itself felt so widely, but I feel that the explanation will eventually be found in studying

the effects of physical conditions upon the animal life, and that no progress is possible until we rid ourselves of our belief in protective coloration, at any rate so far as it is applied generally to desert animals.

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